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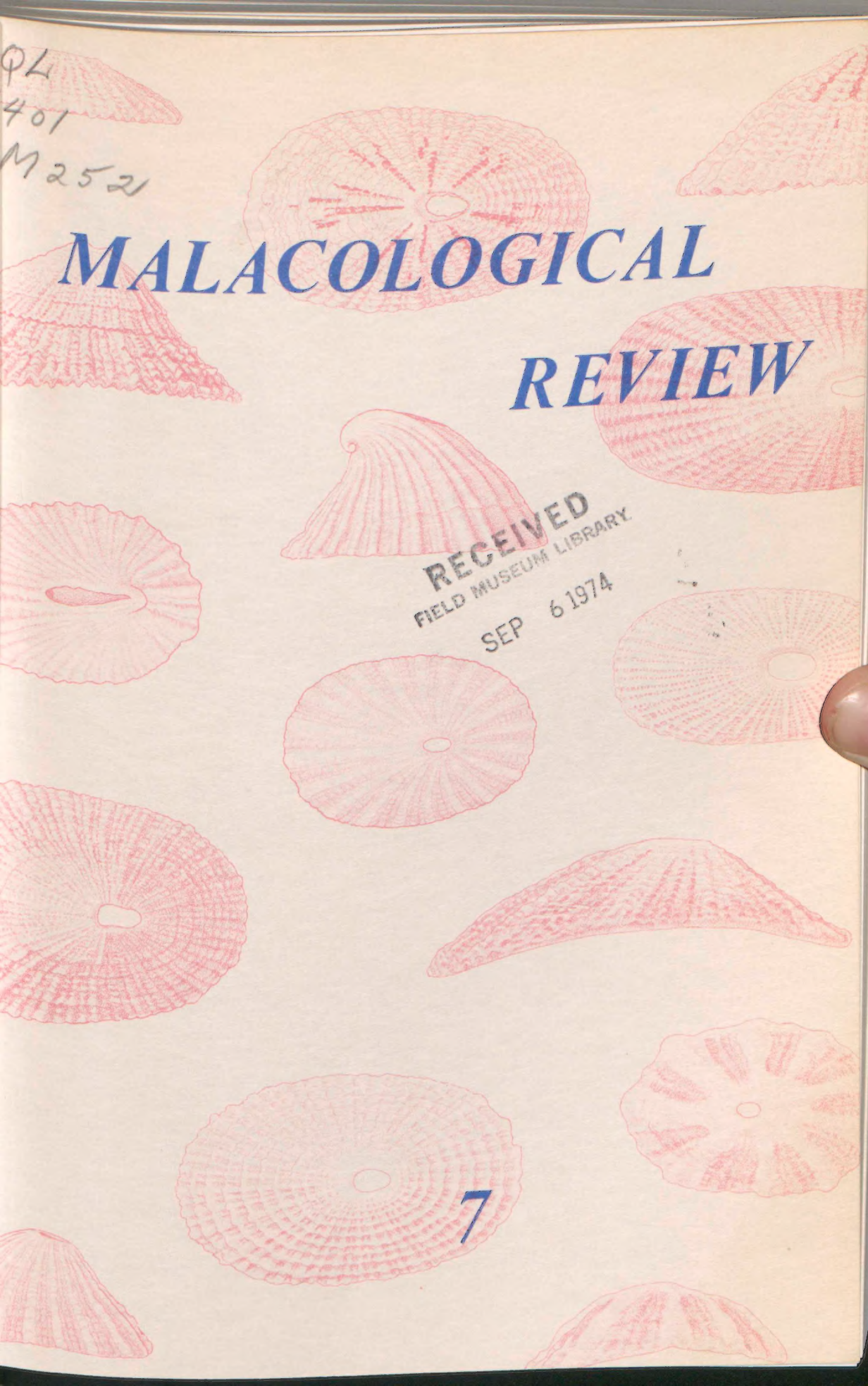

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MALACOLOGICAL REVIEW

P. O. Box 801
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ON THE COVER - Keyhole limpets. Illustrations by John L. Tottenham.

1974

MALACOLOGICAL REVIEW

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1974

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COVER ILLUSTRATIONS FOR *MALACOLOGICAL REVIEW*:

Vol. 1: Succineidae (amber shells)
Vol. 2: *Stagnicola* (Lymnaeidae)
Vol. 3: Epitoniidae (wentletraps)
Vol. 4: Conidae (cone shells)
Vol. 5: *Dysnomia* (freshwater mussels)
Vol. 6: Freshwater gastropods of the Lake Ohrid region, Yugoslavia
Vol. 7: Keyhole limpets

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197293

MALACOLOGICAL REVIEW

VOLUME 7, Number 1 1974

CONTENTS

Research Articles

Note sur la répartition en Belgique de trois mollusques Gastéropodes terrestres peu connus: *Acme inchoata* (Prosobranches, Acmidae), *Abida frumentum* (Stylommatophores, Vertiginidae) et *Alexia denticulata* (Basommatophores, Ellobiidae). S. SEVO 1
Electrophoretic studies on foot muscle esterases of some African *Biomphalaria* species. F. M. A. UKOLI 15
Immunological relationships of two species of Lymnaeidae (Mollusca: Basommatophora) from Macedonia, Yugoslavia. J. B. BURCH and S. HADŽIŠČE 25

Brief Communications

A review of some land snails of the eastern United States. L. HUBRICHT 33
Oviposition in the land snail *Anguispira alternata* (Stylommatophora: Endodontidae). A. TOMPA 35
A colchicine hypotonic squash technique for chromosome spreads of pulmonate land snails. N. BABRAKZAI and W. B. MILLER 37

Proceedings and Abstracts, Mollusk Seminar, Ann Arbor, 1973

Program 40
Systematics, Variation and Zoogeography 41
Anatomical systematics of freshwater mussels. W. H. HEARD 41
Comparative reproduction in viviparid snails. V. A. VAIL 42
Studies on Physidae (Pulmonata: Basommatophora). I. Penial complex morphological groupings. G. A. TE 43
Scanning electron microscope studies of the embryonic shell surface sculpture in *Bulinus*. C. M. PATTERSON 45
Freshwater mollusks of Lake Ohrid, Macedonia. S. HADŽIŠČE, J. B. BURCH and C. M. PATTERSON 47
Growth, Development, Behavior, Physiology and Biochemistry 48
Life table parameters of an experimental population of *Omalonyx felina* (Pulmonata: Succineidae). A. L. SHRADER 48
The structure, ciliation and function of the lips of bivalves. T. H. J. GILMOUR 48
The structure of calcareous snail eggs. A. TOMPA 49
Behavioral and physiological studies on locomotion in the giant garden slug, *Limax maximus*. D. J. PRIOR and A. GELPERIN 50
Comparative aspects of the morphology and physiology of a single identifiable neuron in *Helix aspersa*, *Limax maximus* and *Ariolimax californica*. D. SENSEMAN and A. GELPERIN 51
The histochemical identification of galactogen in the Succineidae. P. H. RUDOLPH 52
Organ culture of *Helix pomatia* albumen gland in a defined medium. E. M. GOUDSMIT and S. L. FELDMAN 53

(continued)

Snails as Intermediate Hosts of Parasites 54
A simple biochemical method for discerning between diploid and polyploid species of the *Bulinus* (*Isidora*) complex. G. K. LINDSAY 54
The genus *Bulinus* and schistosomiasis in North Africa. P. T. LoVERDE 54
Biology and control of *Bulinus truncatus* in Egypt. E. S. DEMIAN and E. G. KAMEL 55
Experimental infection of *Bulinus sericinus* with *Schistosoma haematobium*. S.-K. WU and J. B. BURCH 56
The larval interaction of *Paragonimus ohirai* and *Schistosoma japonicum* in *Oncomelania*. P. T. LoVERDE and M. PARKER. 57

News and Announcements

Meeting of the Institute of Malacology 59
The Conchological Society of Great Britain and Ireland, Program of Meetings for 1974. 59
Deutschen Malakozoologischen Gesellschaft 59
Western Society of Malacologists 60
American Malacological Union 60
Unitas Malacologica Europaea 60
Lerner Marine Laboratory 60
Voucher Specimens 60
Index Animalium 61
EPA Mollusk Identification Manuals 61
Court case to halt construction on dams on the Duck River, Tennessee 62
Mollusk Seminar, Ann Arbor, Michigan 62

Obituary

George Paul Kanakoff 63

Contents of Current Malacological Periodicals 65
Author index for malacological periodicals. 93

Publications. 101

Malacological Review, 1974, 7: 1-14

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NOTE SUR LA REPARTITION EN BELGIQUE DE TROIS MOLLUSQUES GASTEROPODES TERRESTRES PEU CONNUS: *ACME INCHOATA* (PROSOBRANCHES, ACMIDAE), *ABIDA FRUMENTUM* (STYLOMMATOPHORES, VERTIGINIDAE) ET *ALEXIA DENTICULATA* (BASOMMATOPHORES, ELLOBIIDAE)

Slavica Sevo

RESUME

Au cours d'une enquête malacologique menée en 1970 dans quelques provinces de la Belgique, 3 espèces de Gastéropodes peu connues dans le pays ont retenu notre attention: *Acme inchoata* Ehrmann, *Abida frumentum* Draparnaud et *Alexia denticulata* Montagu.

Pour chacune de ces 3 espèces, les caractéristiques chonchiologiques sont comparées avec celles de leur congenères classiques à savoir, *Acme lineata* Draparnaud pour la première espèce, *Abida secale* Draparnaud pour la deuxième et *Alexia myosotis* Draparnaud pour la troisième.

Acme inchoata a été trouvée dans 5 localités au sud de Namur, dans des stations fraîches sur calcaire dévonien. L'espèce semble y avoir atteint sa limite méridionale.

Abida frumentum fut observée dans 4 localités sur les rochers calcaires dévoniens du bassin de la Meuse. L'espèce s'y trouve à proximité de la limite septentrionale de sa distribution. Jusqu'à présent l'existence de cette espèce dans le pays a été considerée comme douteuse.

Alexia denticulata a été trouvée à Nieuport sur la vase des eaux saumâtres. La présence d'un spécimen vivant est signalée pour la première fois en Belgique.

Au cours de l'été 1970, le Groupe de Travail pour l'Etude de la Lutte contre les Limnées[1] a procéde en Belgique à une enquête malacologique effectuée dans la Flandre occidentale, la province de Namur et le nord de la province de Luxembourg.

Les terrains examinés à cette occasion étaient répartis dans différentes régions naturelles du pays. Ils faisaient généralement partie de complexes herbagers; toutefois, certaines stations étaient constituées de milieux boisés ou de terrains non cultivés (terrains rocheux, bords de routes, berges de fossés et de canaux) étant en rapport direct ou indirect avec les pâturages.

La faune malacologique des endroits examinés a été définie par différentes espèces extraites des échantillons de matières prélevés sur la couche superficielle du sol. Chaque échantillon représentait environ 1 kg de matériel composé en grande partie de débris de végétaux, de mousses, d'algues ou de petits phanérogames recouvrant le sol, le restant étant de la boue (terre).

L'extraction des mollusques vivants et des coquilles vides fut effectuée au laboratoire. Le matériel a été d'abord immergé dans l'eau et délayé dans la masse de liquide; le tout a été déversé ensuite au travers de 4 tamis superposés (mailles de dimensions décroissantes: 3, 2, 1 et 0,7 mm) et lavé par des jets d'eau. Le refus des divers tamis a été finalement examiné avec soin pour en retirer chaque mollusque.

---

[1]Ministère de l'Agriculture. Président: W. E. van den Bruel.

Cette méthode est couramment utilisée depuis 1960 par notre groupe et nous a fourni d'excellents résultats dans l'étude de la faune malacologique belge des prairies agricoles. Son application à de très grands nombres d'échantillons fournis par l'étude systématique de terrains répartis dans les diverses régions agricoles de pays, nous a permis de recueillir et d'identifier au cours de 10 années d'énormes quantités de Gastéropodes. La technique de travail nous a permis en outre de connaître la fréquence relative de chaque espèce dans les diverses régions étudiées.

Cette étude montre combien l'usage de la méthode décrite, conçue pour définir de façon quantitative le peuplement malacologique des terrains étudiés, fournit des informations intéressantes qui complètent l'état des connaissances sur la répartition des espèces dans les diverses régions du pays.

Ces rélevés malacologiques feront l'objet de plusieures publications: elles sont actuellement en préparation. Nous voudrions par la présente note faire simplement état de 3 mollusques terrestres peu connus dans le pays et dont la présence dans certains des échantillons, provenant de notre enquête de l'été 1970, mérite d'être signalée. Il s'agit de *Acme inchoata* Ehrmann 1933, *Abida frumentum* Draparnaud 1801 et *Alexia denticulata* Montagu 1803, appartenant respectivement aux Prosobranches, aux Stylommatophores et aux Basommatophores.

I. *Acme inchoata* Ehrmann 1933

Les Acmidae sont de petits Gastéropodes Prosobranches qui font partie du groupe des Pneumonopoma (operculés terrestres) comportant des taxa spécialement adaptés à la vie terrestre.

La coquille des Acmidae est très caractéristique: forme subcylindrique à sommet obtus composée de 5 à 6 tours de spires, ornés à des distances régulières de stries longitudinales creuses (Fig. 1).

Le représentant classique, *Acme lineata* Draparnaud (1801), montre un péristome bien développé avec un bourrelet externe (Fig. 2). *Acme inchoata* s'en distingue par une taille plus petite (2 à 3 mm) et par un péristome très simple, non réfléchi, dont seul le bord columellaire est élargi, ne recouvrant que partiellement l'ombilic. La petite fente, qui caractérise l'espèce précédente à l'insertion supérieure du péristome, fait défaut.

Ehrmann avait observé cette forme typique chez des spécimens provenant d'Angleterre et d'Irlande. Il avait proposé de lui attribuer le nom d'espèce *Acme inchoata*.

Steusloff (1943) signale cette espèce, en Allemagne, dans des hêtraies (*Fagetum* à *Mercurialis perennis* et *Asperula odorata*) établies sur des calcaires oolothiques du versant sud du "Vogelensangbach", affluent sud de la Ruhr. L'espèce se serait dispersée à la période postglaciaire en remontant la vallée du Rhin dont le bassin à cette époque était encore relié au réseau hydrographique de la partie Sud-Est de l'Angleterre.

Acme inchoata appartient donc au groupe des Gastéropodes qui avaient leur refuge en période glaciaire dans la partie Ouest du continent (Ant, 1963). Sa présence dans les peuplements malacologiques confère à ceux-ci un caractère atlantique.

Steusloff voit dans la simplification de l'armature du péristome de *Acme inchoata* un développement parallèle à celui observé chez *Clausilia dubia* Draparnaud 1801 var. *obsoleta*, race géographique de *Clausilia dubia*, laquelle serait typique des pays occidentaux et de l'Angleterre. Par analogie, *Acme inchoata* serait une race géographique de *Acme lineata*, établie en Europe occidentale.

En ce qui concerne la Belgique, *Acme inchoata* a été signalée sous le nom de *Acme lineata* dans 3 localités situées aux environs de Bruxelles et à Bouvignes, près de Dinant dans la vallée de la Meuse (Adam, 1960).

Nous avons trouvé le mollusque à plusieurs reprises dans la vallée de la Meuse au sud de Namur et le long des affluents secondaires découpant les plateaux famenniens et condrusiens (Fig. 9). Sur un total de 40 échantillons prélevés dans 18 localités, le mollusque fut retrouvé dans 5 de celles-ci. Le Tableau 1 montre pour chacun des échantillons le nombre de spécimens (individus vivants et coquilles vides) et la composition du peuplement malacologique auquel le mollusque appartient. Ce même tableau donne une brève description des stations dans lesquelles ces échantillons ont été prélevés. Il s'agit en général de bois (hêtraies) établis sur calcaires dévoniens et sur psammites et schistes du dévonien supérieur (Famennien), où le mollusque occupe les endroits frais des versants à proximité des affluents secondaires; on a récolté les specimens sous les feuilles mortes.

Au sujet de la répartition de ce Gastéropode dans les régions vallonnées de la Meuse, nous trouvons une parfaite correspondance avec les observations de Steusloff effectuées dans la vallée accidentée de la Ruhr. *Acme inchoata* semble avoir atteint dans ces régions sa limite méridionale de dispersion; la forme de *Acme lineata* s. str., qui est d'origine adriato-méditerranéenne (Ant, 1963), est plutôt représentée autour des Alpes; cette espèce ne semble pas jusqu'à présent avoir pénétré dans nos régions.

La présence de *Acme inchoata* dans la partie accidentée du bassin de la Meuse montre que les peuplements malacologiques de cette région sont nettement influencés par des infiltrations atlanto-britanniques.

A cet égard, l'espèce *Acme inchoata* constitue un élément fort important pour la faune malacologique belge.

II. *Abida frumentum* Draparnaud 1801

Le genre *Abida* comporte en Belgique 2 espèces: *Abida secale* Draparnaud 1801 et *Abida frumentum* Draparnaud 1801.

Ces mollusques ont des coquilles très caractéristiques (Figs. 3 et 4), fusiformes avec un nombre important de tours de spires (9 à 10). Le péristome est pourvu d'une denticulation très complexe comportant une longue lamelle angulaire, des lamelles pariétales et columellaires, un pli basal et ordinairement des plis accessoires (Germain, 1930).

Les 2 espèces se distinguent d'une façon très nette par le péristome ayant un gros bourrelet blanc externe chez *Abida frumentum;* cette formation n'est pas apparente chez *Abida secale*. De même, la denticulation de *Abida frumentum* est plus épaisse et plus profonde que celle de *Abida secale;* sa coquille est aussi plus globuleuse.

D'après Adam (1960), *Abida secale* est très commun dans la région calcaire du bassin de la Meuse. Par contre, *Abida frumentum* n'a été récolté qu'une seule fois dans la région de Fosse. Cet auteur considère la présence de cette dernière comme douteuse pour la Belgique.

Les 2 espèces ont une origine méditerranéenne: en période glaciaire *Abida secale* aurait eu ses refuges dans le Sud-Ouest tandis qu'*Abida frumentum* serait plutôt une espèce issue de la zone adriato-méditerranéenne (Ant, 1963).

La progression postglaciaire de la première espèce vers le Nord s'est effectuée sans difficulté le long de la zone atlantique, bénéficiant d'un climat tempéré et humide. La pénétration de ce mollusque vers l'intérieur du continent a eu lieu à partir de la zone Ouest de l'Europe au cours de la période très humide de l'Atlanticum.

Par contre, *Abida frumentum*, issu des refuges adriato-méditerranéens, n'a pas eu les mêmes facilités pour progresser vers le Nord. L'aire géographique de cette espèce s'est disloquée dans les régions montagneuses des Alpes.

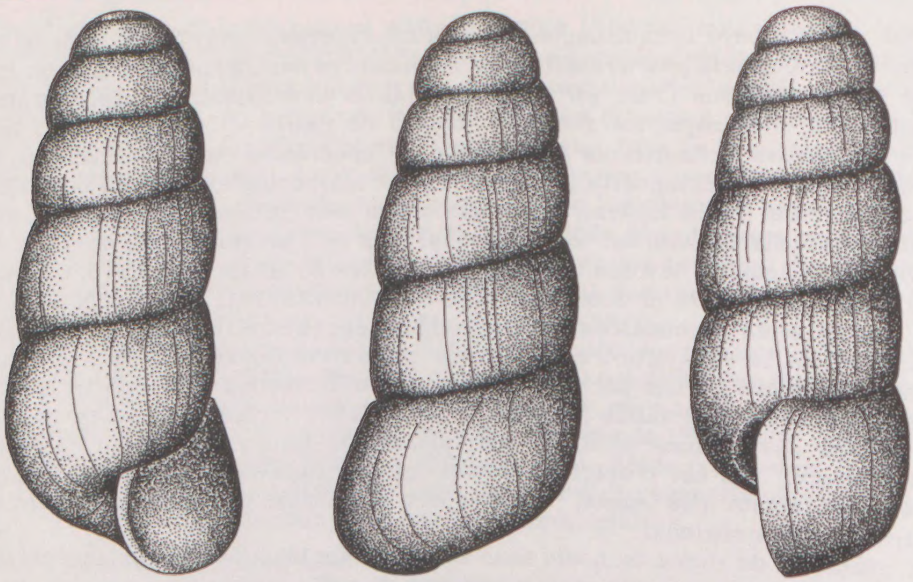


FIG. 1. *Acme inchoata* Ehrmann 1933; h = 3 mm; Feschaux, le 29 juin 1970.

FIG. 2. *Acme lineata* Draparnaud 1801; h = 3,5 mm; Interlaken (Suisse), le 23 juillet 1971.

Au cours de notre enquête dans la vallée de la Meuse, nous avons trouvé *Abida frumentum* sur les rochers du versant gauche de la Meuse entre Namur et Dinant (Namur, Profondville, Rivière et Dinant, voir Fig. 10) sur des calcaires carbonifères et frasniens à exposition sud. Ces rochers étaient généralement couverts d'un taillis assez clairsemé (Fig. 7). Le Tableau 2 donne une brève description de ces endroits ainsi que le nombre d'individus repérés dans nos échantillons.

La progression de *Abida frumentum* jusqu'au complexe calcaire du bassin de la

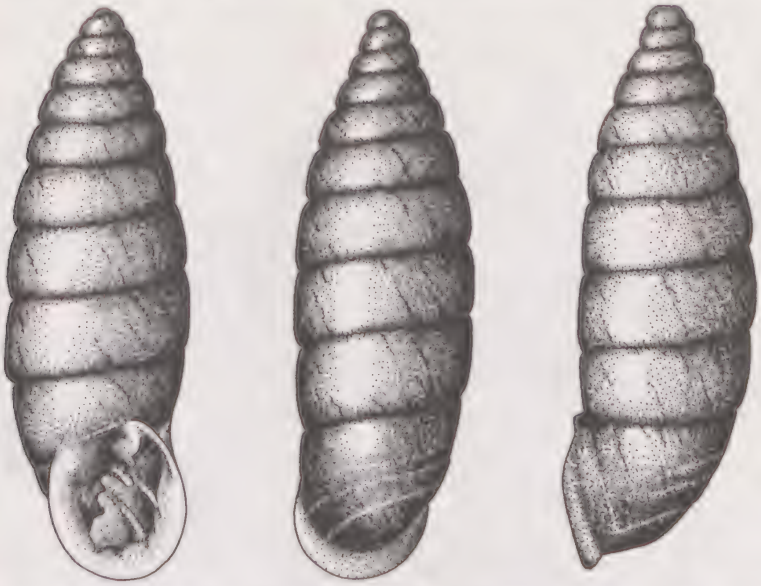


FIG. 3. *Abida frumentum* Draparnaud 1801; h = 10 mm; Dinant, le 17 juillet 1968.

FIG. 4. *Abida secale* Draparnaud 1801; h = 7 à 8 mm; Rivière, le 17 juillet 1968.

Meuse constitue un fait très interessant. Le mollusque, étant à la limite septentrionale de sa distribution, ne s'observe que dans les habitats bénéficiant d'un microclimat optimal (rochers calcaires constituant des endroits bien exposés au réchauffement). Par contre *Abida secale*, ayant une origine atlanto-méditerranéenne, est visiblement plus répandu dans le pays.

III. *Alexia denticulata* Montagu 1803

Le genre *Alexia* est représenté en Belgique par 2 espèces: *Alexia myosotis* Draparnaud 1801 et *Alexia denticulata* Montagu 1803.

Il s'agit de Gastéropodes dont la coquille (hauteur 7 à 8 mm) a une forme très

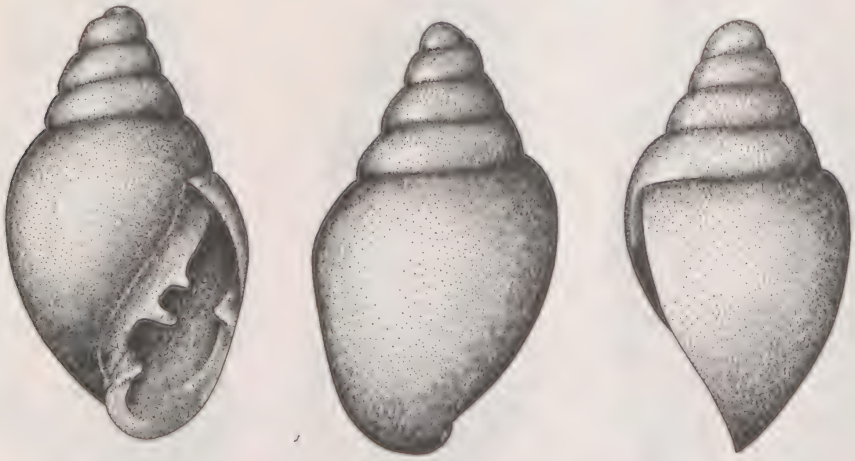


FIG. 5. *Alexia denticulata* Montagu 1803; h = 4 mm; Nieuport, le 22 juin 1970.

FIG. 6. *Alexia myosotis* Draparnaud 1801; h = 5,5 à 7,5 mm; Nieuport, le 22 juin 1970.

typique, fusiforme et allongée (Figs. 5 et 6); le péristome piriforme est garni d'un pli columellaire bien développé au dessus duquel il y a quelques plis pariétaux.

Les 2 espèces se distinguent d'une façon très nette par l'armature du bord extérieur du péristome, lequel est pourvu de 5 à 6 plis pariétaux chez *Alexia denticulata*. La Figure 5 représente un jeune spécimen de *Alexia denticulata* chez lequel les plis pariétaux ne sont pas encore complètement développés; ces plis font défaut chez *Alexia myosotis*.

Parmi les Ellobiidae (Basommatophores terrestres) le genre *Alexia* a conservé ses relations primitives avec le milieu littoral: en effet, on retrouve ces mollusques à proximité de la mer et sur la vase des eaux saumâtres subissant l'effet des marées.

Alexia myosotis est assez commun; par contre, *Alexia denticulata* s'est révélé beaucoup plus rare. D'après Adam (1960), l'espèce n'aurait pas encore été trouvée vivante dans le pays.

Au cours de notre enquête dans la région de Nieuport (Fig. 11), nous avons trouvé un spécimen vivant dans un échantillon prélevé le long du canal de l'Yser dans le dépôt d'algues entre les rocailles (Fig. 8). Un deuxième échantillon, prélevé au même endroit renfermait une coquille vide.

FIG. 7. Calcaire dévonien, couvert d'un taillis clairsemé; habitat de *Abida frumentum* - Rivière.

FIG. 8. Berge du canal de l'Yser; habitat de *Alexia denticulata* - Nieuport.

TABLEAU 1. Description des stations hébergeant *Acme inchoata* Ehrmann 1933.

Grid Ref. *	Communes	Assises géologiques	Description du terrain	Resultat analyse échantillons	
				Nombre *A. inchoata*	Autres espèces
FR 27	Denée-Maredsous	Calcaire carbonifère (Dinantien)	Futaie (noisetier et hêtre) située dans une dépression creusée dans le calcaire (sol frais). Echantillon pris sous les feuilles mortes le long de la route. Exposition Nord.	3 vivants	*Discus rotundatus* *Vallonia pulchella* *Acanthinula aculeata* *Carychium tridentatum* *Clausilia parvula* *Retinella nitidula*
FR 28	Arbre	Calcaire du Dévonien moyen (Givetien)	Bois sur fond rocheux. Echantillon pris sous les feuilles mortes le long de la route.	1 vivant	*Pomatias elegans* *Oxychilus draparnaudi* *Vitrea crystallina* *Retinella nitidula* *Discus rotundatus* *Punctum pygmaeum* *Ena obscura* *Trichia hispida* *Helicella itala* *Acanthinula aculeata* *Helicodonta obvoluta* *Carychium tridentatum*
FR 36	Heer-Blaimont	Série psammitique du Dévonien supérieur (Famennien supérieur)	Bois sur le versant rocheux de la Meuse. Echantillon pris sous des pierres (roches). Exposition Est.	2 vivants	*Cepaea hortensis* *Zenobiella incarnata* *Clausilia nigricans* *Succinea putris* *Cochlicopa lubrica* *Trichia sericea* *Vertigo pygmaea*

TABLEAU 1. (Cont.)

Grid Ref. *	Communes	Assises géologiques	Description du terrain	Resultat analyse échantillons	
				Nombre *A. inchoata*	Autres espèces
					Vallonia costata *Cecilioides acicula* *Carychium minimum* *Vallonia pulchella* *Punctum pygmaeum* *Vitrina major*
FR 35	Feschaux	Schiste du Dévonien supérieur (Famennien supérieur)	Bois dans une vallée secondaire. Echantillon pris sous les feuilles mortes au fond d'un fossé secondaire. Exposition Nord.	3 vivants	*Lymnaea truncatula* *Succinea oblonga* *Discus rotundatus* *Carychium tridentatum* *Trichia sericea* *Punctum pygmaeum*
FR 36	Waulsort	Série psammitique du Dévonien supérieur (Famennien supérieur)	Bois sur fond rocheux du versant de la Meuse. Echantillon pris sous les feuilles mortes dans le lit sec d'un petit affluent secondaire descendant vers la vallée principale.	2 vides	*Vitrea crystallina* *Helicodonta obvoluta* *Cochlicopa lubrica* *Helix pomatia* *Clausilia parvula* *Discus rotundatus* *Pomatias elegans* *Euconulus fulvus* *Cochlodina laminata* *Punctum pygmaeum* *Retinella nitidula* *Orcula doliolum*

*Quadrillage U. T. M., voir Fig. 9.

TABLEAU 2. Description des stations hébergeant *Abida frumentum* Draparnaud 1801.

Grid Ref.*	Communes	Assises géologiques	Description du terrain	Resultat analyse échantillons	
				Nombre *A. frumentum*	Autres espèces
FR 39	Namur	Calcaire carbonifère	Citadelle, rochers à exposition Sud, taillis du bois.	2 vivants 1 vide	*Oxychilus draparnaudi* *Cepaea hortensis* *Clausilia parvula* *Vitrea crystallina* *Vitrina major* *Pyramidula rupestris* *Zenobiella incarnata*
FR 38	Profondville	Calcaire frasnien	Rochers sur le versant gauche de la Meuse. Exposition Sud. Taillis de bois.	1 vivant 1 vide	*Cepaea nemoralis* *Fruticicola fruticum* *Helicella itala* *Succinea putris* *Oxychilus draparnaudi* *Cepaea hortensis* *Helicodonta obvoluta* *Cochlicopa lubrica* *Clausilia parvula* *Laurria cylindracea* *Pupilla muscorum* *Vallonia costata* *Cecilioides acicula* *Vertigo pusilla* *Vertigo pygmaea* *Abida secale*
FR 38	Rivière	Calcaire frasnien	Rochers sur le versant gauche de la Meuse. Exposition Sud.	1 vivant	*Lymnaea peregra* *Clausilia parvula*

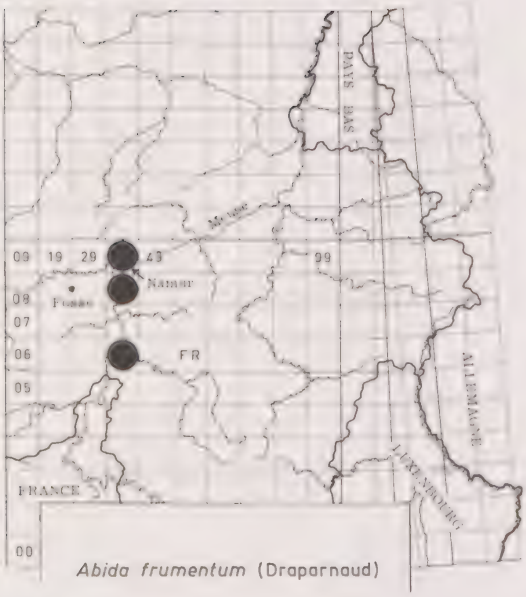
TABLEAU 2. (Cont.)

Grid Ref. *	Communes	Assises géologiques	Description du terrain	Resultat analyse échantillons	
				Nombre *A. frumentum*	Autres espèces
			Taillis de bois.	1 vide	*Pomatias elegans* *Cochlicopa lubrica* *Oxychilus draparnaudi* *Helix pomatia* *Helicella itala* *Vallonia costata* *Cecilioides acicula* *Vertigo pygmaea* *Lauria cylindracea* *Pupilla muscorum*
FR 36	Dinant	Calcaire dinantien	Rochers en bordure de la route dans le vallée de la Meuse. Taillis de bois.	3 vides	*Fruticicola fruticum* *Pomatias elegans* *Cecilioides acicula* *Pupilla muscorum* *Vallonia costata* *Orcula doliolum* *Helicodonta obvoluta* *Cochlodina laminata* *Iphigena ventricosa* *Helicella itala* *Abida secale* *Clausilia parvula* *Trichia hispida* *Vitrea crystallina* *Oxychilus draparnaudi*

*Quadrillage U. T. M., voir Fig. 10.

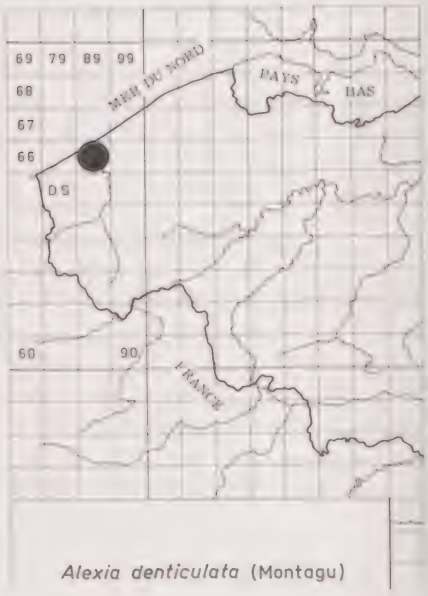
Acme inchoata (Ehrmann)

9



Abida frumentum (Draparnaud)

10



Alexia denticulata (Montagu)

11

TABLEAU 3. Description des stations hébergeant *Alexia denticulata* Montagu 1803.

Grid Ref. *	Commune	Assises géologiques	Description du terrain	Resultat analyse échantillons	
				Nombre *A. denticulata*	Autres espèces
DS 86	Nieuport (Remblais) (Berge)	Sable holocène région des dunes	Echantillon pris entre les joints des briques, dépôts d'algues, sable humide, à 3 m de niveau d'eau. Exposition Nord-Est.	1 vivant 1 vide	*Trichia hispida* *Trichia sericea* *Cochlicella acuta* *Helicella virgata* *Helicella profuga* *Helicella cespitum* *Oxychilus cellarius* *Oxychilus draparnaudi* *Zonitoides nitidus* *Spiralina vortex* *Tropidiscus planorbis* *Anisus rotundatus* *Bathiomphalis contortus* *Discus rotundatus* *Bithynia tentaculata* *Bithynia leachi* *Hydrobia jenkinsi* *Hydrobia ulvae* *Pupilla muscorum* *Lauria cylindracea* *Cochlicopa lubrica* *Valvata piscinalis* *Vallonia pulchella* *Alexia myosotis* *Buccinum undatum* *Punctum pygmaeum* *Hydrobia stagnorum* *Valvata cristata* *Tropidiscus carinatus* *Segmentina nitida* *Assiminea grayana* *Lymnaea peregra* *Vallonia costata* *Vitrina major* *Cecilioides acicula*

*Quadrillage U. T. M., voir Fig. 11.

L'espèce ne semble donc pas avoir établi des populations importantes, mais dès à présent on peut la considérer comme un élément définitif de la faune malacologique belge.

Cette étude montre que l'examen malacologique des terrains fournit des resultats très intéressants dans certaines régions de la Belgique.

Les calcaires dévoniens du bassin de la Meuse offrent de nombreux habitats très favorables dans lesquels certains Gastéropodes d'origine méridionale et alpestre atteignent la limite septentrionale de leur distribution géographique (*Abida frumentum*).

Ce même bassin héberge d'autres espèces d'origine atlanto-britannique (*Acme inchoata*) dont la progression vers le Sud et le Sud-Est semble être contrariée par la continentalité croissante du climat.

Dans cette optique il importe d'accorder aux calcaires dévoniens du Sud de la Belgique une attention particulière.

La découverte d'un spécimen vivant d'*Alexia denticulata* à Nieuport montre également l'importance qu'il faut attribuer aux Gastéropodes littoraux de cette région.

ABSTRACT

The author reports on the occurrence of 3 gastropod species of previously doubtful occurrence in Belgium: *Acme inchoata* Ehrmann, *Abida frumentum* Draparnaud and *Alexia denticulata* Montagu.

These species have been noted during malacological investigations carried out in 1970 in western Flanders and in Namur and northern Luxembourg provinces. Conchological characteristics of the 3 species were compared to those of their respective classical congeners, i. e., *Acme lineata* Draparnaud, *Abida secale* Draparnaud and *Alexia myosotis* Draparnaud.

Acme inchoata was found on calcareous Devonian in 5 humid locations south of Namur, a finding which confirms the presence of this species in Belgium. These sites seem to represent the southern limit of the species.

Abida frumentum was observed in 4 sites on calcareous Devonian rocks of the Meuse basin. These sites are close to the northern distribution limit of this species. Its presence in this country was doubtful until now.

Alexia denticulata was found in Nieuport on brackish water ooze. The presence of a living specimen in Belgium is reported for the first time.

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ELECTROPHORETIC STUDIES ON FOOT MUSCLE ESTERASES OF SOME AFRICAN *BIOMPHALARIA* SPECIES[1]

F. M. A. Ukoli[2]

ABSTRACT

The electrophoretic patterns of foot muscle esterases of snails from 6 populations of *Biomphalaria pfeifferi* and 1 population each of *B. alexandrina* and *B. sudanica* from different parts of Africa were investigated using disc electrophoresis. This study revealed a characteristic pattern common to all the individuals from the various populations, but there are differences sufficiently marked and consistent to distinguish one population from the others. It was, however, not possible to distinguish the 3 species on the basis of their esterase patterns. These findings were compared with the results of other workers using digestive gland esterases.

INTRODUCTION

During the last decade, interest in cytological and biochemical characters of planorbid snail vectors of human schistosomes has been shown by quite a few workers. This is not only because morphological characters alone have been unsatisfactory in elucidating the taxonomy of the group, but also because differences in susceptibility to infection have been detected at the population level, even when no obvious morphological differences seemed to exist. Thus Burch (1964) showed a correlation between chromosome numbers in *Bulinus* s.s. and susceptibility with *Schistosoma haematobium*, and later Burch & Lindsay (1967) found a correlation between electrophoretic patterns of foot muscle esterases and chromosome numbers.

Wright & Ross (1965) showed that planorbid egg proteins, when subjected to electrophoresis, were sensitive indicators of differences at the population level. Wright, File & Ross (1966), using starch gel electrophoresis, tested various organs of planorbid snails for distribution of enzymes and found that the digestive gland was the richest in esterases, although these may be affected by the age and dietary condition of the snail. Also, using the same techniques, Wright & File (1968) working with *Bulinus*, Malek & File (1971) working with *Biomphalaria* from the Neotropics and Wium-Andersen (1973) working with some African *Biomphalaria*, all showed variations in digestive gland esterases between snail populations.

The present study involved the use of disc electrophoresis to investigate foot muscle esterases of 6 populations of laboratory-reared *Biomphalaria pfeifferi* and 1 population each of *B. sudanica* and *B. alexandrina* from various parts of Africa, maintained in the Mollusk Division, Museum of Zoology, The University of Michigan. Previous electrophoretic studies of African *Biomphalaria* utilizing starch gel are by Wright, File & Ross (1966), who found that foot muscle was one

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of the organs poorest in esterases and that digestive gland esterases showed "considerable amount of unexplained variation even between individuals of comparable age and dietary background" in *B. sudanica*, and Wium-Andersen (1973), who used digestive gland of several species of *Biomphalaria*. In the present study it was decided to use disc electrophoresis on foot muscle extract, because Davis & Lindsay (1967) showed differences in patterns at the population level and that size (age), change of diet and climate have no effect on the esterase patterns using this technique. My results were presented at the Mollusk Seminar held in Ann Arbor in 1972 and a brief abstract appeared in Ukoli (1973).

MATERIALS AND METHODS

The specimens used in this study were obtained from cultures of snails originally collected from different parts of Africa and maintained in the Mollusk Division of the Museum of Zoology, The University of Michigan, Ann Arbor. Eight populations were studied as follows:

1. Population Biom. 14 - *B. alexandrina alexandrina* collected by B. C. Dazo from Egypt in March 1963.
2. Population Biom. 18 - *B. pfeifferi* collected by G. Sevilla from the Pesticide Research Institute near Arusha, Tanzania in October 1963.
3. Population Biom. 21 - *B. pfeifferi* collected by R. E. Kuntz, 3-4 miles from Nairobi, Kenya in October 1964.
4. Population Biom. 22 - *B. pfeifferi* collected by J. B. Burch from Gwebi River, Little England Farm near Salisbury, Rhodesia in March 1965.
5. Population Biom. 28 - *B. pfeifferi* collected by J. B. Burch from Mwanza pool, 20 yds. from Lake Victoria, Tanzania in April 1965.
6. Population Biom. 36 - *B. pfeifferi* collected by W. Sodeman from Liberia in November 1968.
7. Population Biom. 37 - *B. pfeifferi* collected by J. B. Burch from Toquor River at Mekerka, Ethiopia in June 1969.
8. Population Biom. 39 - *B. sudanica* collected by C. T. Lo from Lake Awasa, Ethiopia in October 1971.

The method of disc electrophoresis employed by Davis & Lindsay (1967) for foot muscle extract of molluscs and adapted by Lindsay (pers. comm., 1972) for the study of individual variations in populations of small snails was used. Altogether, 12 individuals from each population of a size previously determined to yield 0.006-0.008 gm of foot muscle were selected. At first, tests were run with 6 snails from each of the 8 populations. Then the procedure was repeated with another set of 6 snails.

Each foot was homogenized in 0.2 ml distilled water, using a sonic homogenizer. Then the homogenate was mixed with 0.4 ml "sample" gel solution and centrifuged for about 5 minutes at 1,500 r.p.m. at 0°C. The supernatant was added on top of the "spacer" gel above the lower gel made of 7.5% acrylamide solution which had polymerized. After electrophoresis, the gels were removed from their glass tubes, stained for non-specific esterases and stored in 7% acetic acid.

The gel columns with stained esterase bands were inspected visually and Rf values for each of the various protein bands were determined by direct measurements. Also, densitometric tracings were made with the Photovolt "Densicord" electrophoresis densitometer which also marked off the limits of the fractions and recorded their density units by means of an integrator.

RESULTS

Photographs of representative gels and their densitometric tracings are shown in Figs. 1-4. A total of 10 components, represented by stained bands labelled 1-10, are found, with peaks A-J in the densitometric tracings. Rf values of each of

TABLE 1. Showing mean Rf values for the various esterase bands for the different populations.

Population	Band No. and corresponding Rf value									
	1	2	3	4	5	6	7	8	9	10
Ethiopian (39)	–	–	0.292	–	–	0.534	–	–	0.795	0.846
Rhodesian (22)	–	–	0.303	–	–	0.555	–	–	0.851	0.892
Egyptian (14)	–	–	0.296	–	–	0.545	0.635	0.706	0.800	0.849
Liberian (36)	–	–	0.307	–	–	0.548	0.672	0.752	0.828	0.879
Ethiopian (37)	–	0.169	0.308	–	–	0.560	0.648	0.724	0.855	0.896
Tanzanian (18)	–	–	0.236 0.308 0.344	–	–	0.563	0.673	0.748	0.836	0.885
Tanzanian (28)	–	–	0.253 0.296 0.312 0.341	–	–	0.549	0.669	0.731	0.808	0.860
Kenyan (21)	–	–	0.236 0.294 0.310 0.348	–	–	0.552	0.682	–	0.846	0.898

the bands for each population are shown in Table 1 and represent the mean Rf values of the 12 individuals sampled from each population.

Individuals of the various populations of *Biomphalaria pfeifferi* were found to possess 4 heavily stained bands: 3, 6 and the twin bands 9 and 10 (with the peaks C, F and I and J, respectively). These 4 bands were also present in the populations of *B. sudanica* and *B. alexandrina*. Variations, however, existed between populations, each population being characterized by the prominence, presence or absence of band 7 or 8 (peaks G and H), or the resolution of band 3 into 2-3 smaller bands with peaks designated C_1, C_2, C_3, C_4.

In analyzing the patterns, the following observations were made:

1. Some bands were not discernible on visual inspection of the gels, but their peaks were marked in the densitometric tracings, e.g., Fig. 1b, peaks H, G, E and D. However, some of the peaks (particularly H, G and D), which were pronounced and characteristic of some populations, were faint and appeared merely as traces in others, e.g., Fig. 2a and Fig. 1c.

2. The first band from the origin, marked by peak A, was usually hazy and fuzzy and its presence was difficult to determine, so it is omitted in a consideration of the patterns.

3. Some of the bands may show single peaks in some individuals and double peaks in others, and these may or may not be marked by the integrator, e.g., peaks J, H, G in the Liberian population. These may be 2 diffuse bands which are resolved in some individuals and not in others.

4. Within a given population, there may be a gradation in the prominence of some peaks, e.g., in the Ethiopian population, peaks H and B (Fig. 2), and the Kenyan population, peak G (Fig. 4).

5. In the Kenyan and 2 Tanzanian populations, the band 3, which was represented by a single peak C in all the other populations, was resolved into a number of bands with peaks designated C_1, C_2, C_3, C_4, and these were characteristic of these populations.

Altogether 7 patterns of esterase bands could be recognized, and these fall into 2 broad groups:

Group A - Those whose band 3 had a single peak C.

Pattern I. This pattern showed only the 4 heavily stained bands 3, 6, 9 and 10 characteristic of the species, with traces of peaks H and G and E and D, but these were, however, not visible on visual inspection of the gels (Fig. 1a,b). All the individuals from the populations from Ethiopia (Biom. 39) and from Rhodesia (Biom. 22) possessed this pattern.

Pattern II. Found in population from Egypt (Biom. 14). This was characterized by the relative prominence of peaks H and G. In some individuals (Fig. 1c), the peaks were clear and about equal, but the bands were faint and hardly visible, while in others (Fig. 1d) the bands were more pronounced visually.

Pattern III. Found in the population from Liberia (Biom. 36). This was very similar to pattern II but was characterized by a denser band 7 with a much more prominent peak G than H. Also, the bands 7, 8 and 10 showed double peaks (Fig. 2a), while they were single in other populations.

Pattern IV. Found in the population from Ethiopia (Biom. 37). Here the characteristic was the presence of band 2, found in no other population, which may be very dense with a prominent peak B (Fig. 2d) or faint with a well marked peak in the densitometric tracing (Fig. 2b,c). Another distinguishing feature was that peak H was always more pronounced than G, so that band 8 appeared more heavily stained (Fig. 2b,c,d). Note that this is the opposite of pattern III above.

Group B - Those whose band 3 was resolved into a number of bands with peaks designated C_1, C_2, C_3, C_4.

Pattern V. Found in population from Tanzania (Biom. 18). Here band 3 was resolved into 2-3 bands with peaks C_1, C_2, C_4. Band 4 was faint but its peak D was clearly marked in the densitometric tracings. In some individuals (Fig. 3a), peak H is prominent while G is inconspicuous, while in others both peaks are almost equal (Fig. 3b).

Pattern VI. Found in population from Tanzania (Biom. 28). Here 3-4 peaks (C_1, C_2, C_3, C_4) were clear (Fig. 3c,d) but D was inconspicuous. Also bands 7 and 8 were faint and their peaks H and G almost equal.

Pattern VII. Found in population from Kenya (Biom. 21). This was characterized by the complete absence of band 8 (no trace of peak H), and peak G was either very prominent (Fig. 4a) or slightly so (Fig. 4b). In some individuals (Fig. 4c), peak D was very prominent, while in others (Fig. 4a) it is inconspicuous.

DISCUSSION

The present study shows that *Biomphalaria pfeifferi* is characterized by the presence of 4 heavily stained bands: twin bands near the front, 1 in the middle and 1 near the origin. It also shows that the esterase pattern differs from one

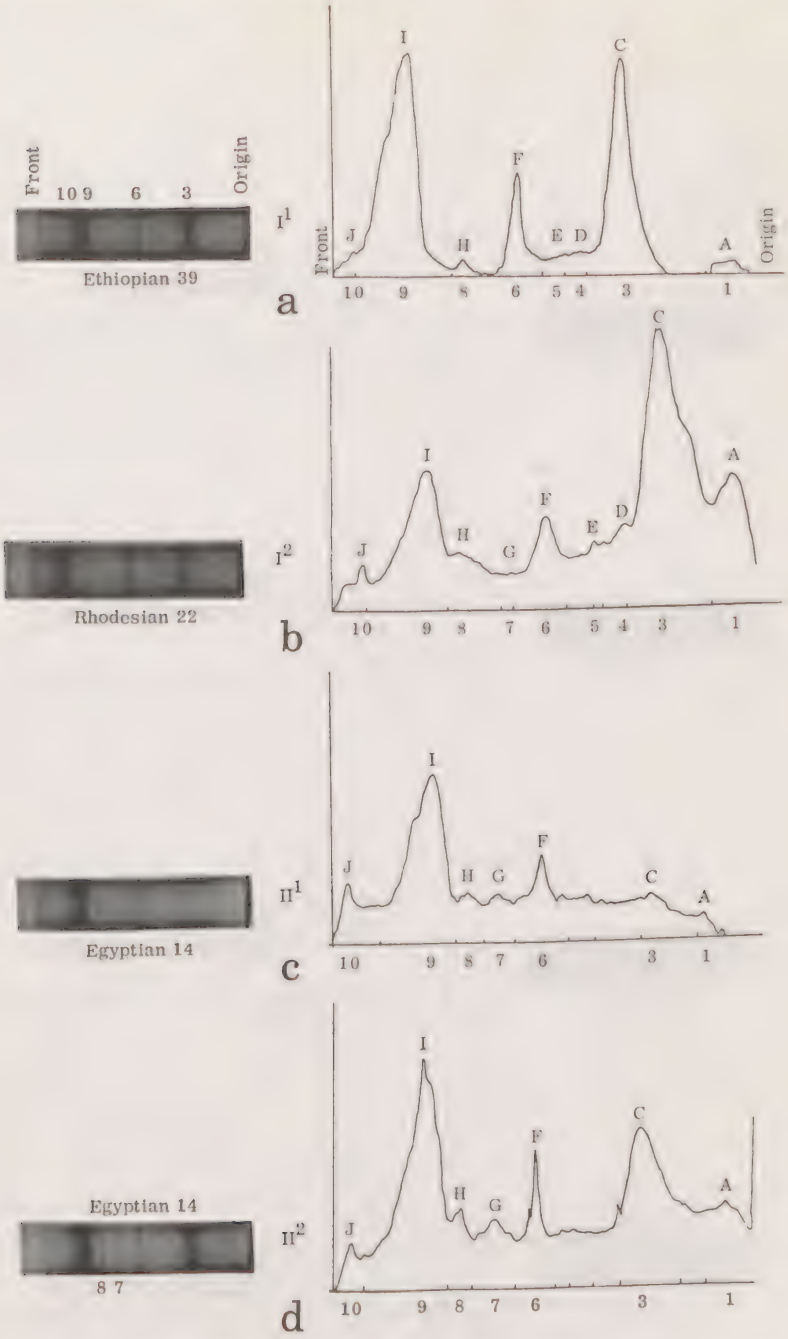

FIG. 1. Electrophoretic patterns of foot muscle esterases and their corresponding densitometric tracings for (a) Ethiopian (39) population of *Biomphalaria sudanica*, (b) Rhodesian (22) population of *B. pfeifferi* and (c, d) Egyptian (14) population of *B. alexandrina*. The letters on the peaks of the densitometric tracings correspond to the numbers of the stained bands of the acrylamide gel columns to the left of each graph. The Roman numerals refer to the banding patterns discussed on p 18.

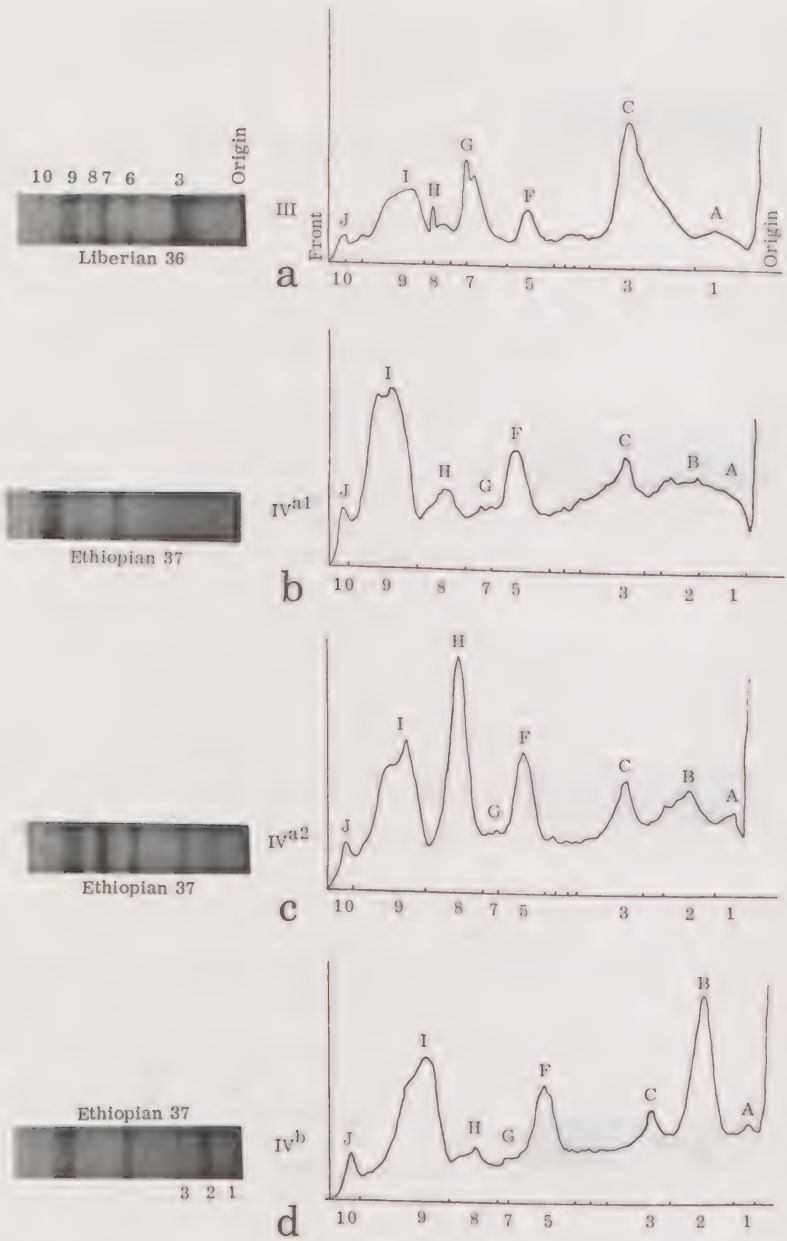

FIG. 2. Electrophoretic patterns of foot muscle esterases and their corresponding densitometric tracings for *Biomphalaria pfeifferi* from (a) Liberian (36) population and (b, c, d) Ethiopian (37) population. The letters on the peaks of the densitometric tracings correspond to the numbers of the stained bands of the acrylamide gel columns to the left of each graph. The Roman numerals refer to the banding patterns discussed on p 18.

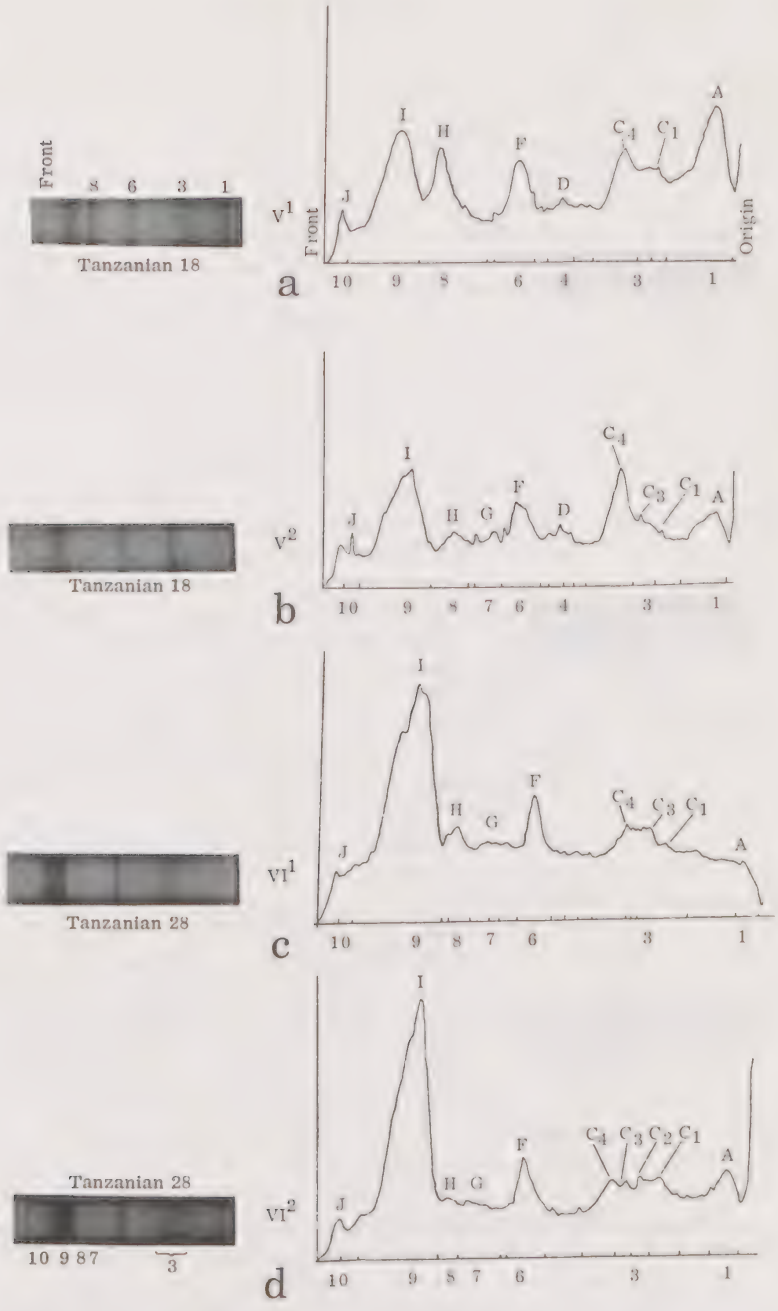

FIG. 3. Electrophoretic patterns of foot muscle esterases and their corresponding densitometric tracings for *Biomphalaria pfeifferi* from (a, b) Tanzanian (18) population and (c, d) Tanzanian (28) population. The letters on the peaks of the densitometric tracings correspond to the numbers of the stained bands of the acrylamide gel columns to the left of each graph. The Roman numerals refer to the banding patterns discussed on p 18.

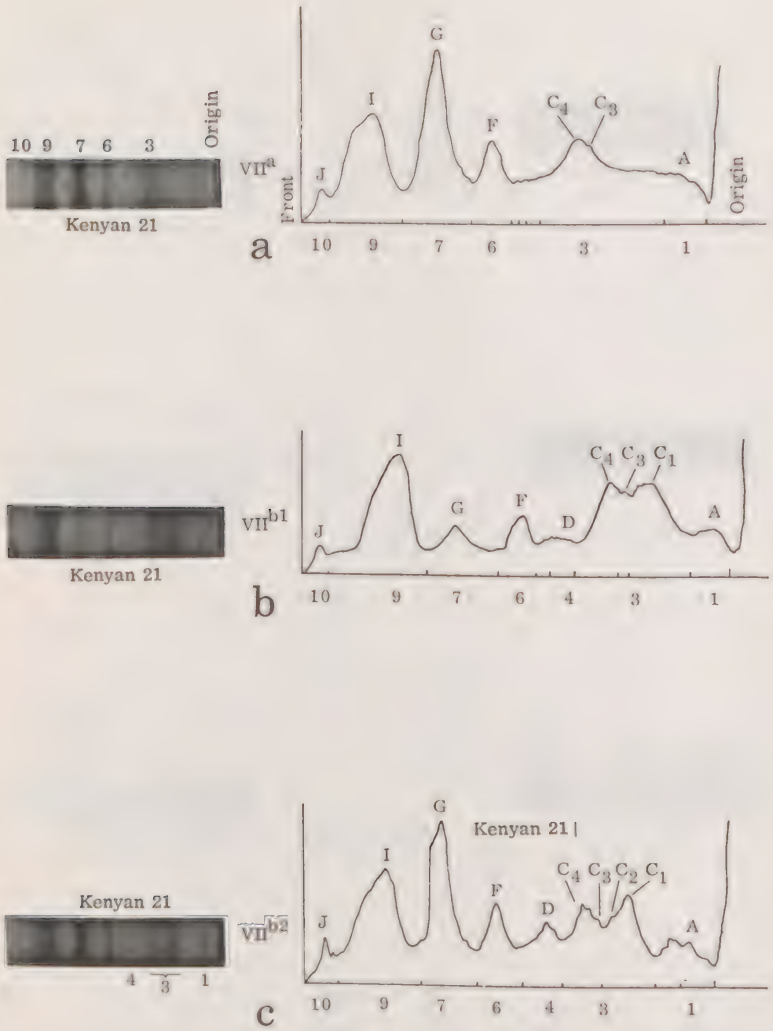

FIG. 4. Electrophoretic patterns of foot muscle esterases and their corresponding densitometric tracings for *Biomphalaria pfeifferi* from the Kenyan (21) population. The letters on the peaks of the densitometric tracings correspond to the numbers of the stained bands of the acrylamide gel columns to the left of each graph. The Roman numerals refer to the banding patterns discussed on p 18.

population to the other. These population differences may be marked, as in the resolution of band 3 into 2-4 smaller bands in the Kenyan and 2 Tanzanian populations, while it remains single in the others. Other population differences include the absence of band 8 in the Kenyan population and its presence in the Tanzanian populations, and the prominence of band 7 in the Liberian population as opposed to the prominence of band 8 in the Ethiopian 37 population. Also, the Rf values for some of the bands differ in the different populations (Table 1). Sometimes, the differences were slight but consistent, involving qualitative variation in the degree of staining, as for example, the presence of bands 7 and 8 at equal intensity in the Egyptian population and the relative density of one or the other in the Liberian and Ethiopian 37 populations. Nevertheless, each population seemed to have a recognizable pattern of its own which, however, was a variant of the basic pattern characteristic of the species.

The Ethiopian population of *Biomphalaria sudanica* and the Egyptian population of *B. alexandrina* also showed a similar characteristic pattern of esterases to *B. pfeifferi*; in fact, *B. sudanica* was practically identical with the Rhodesian population of *B. pfeifferi* (Fig. 1a,b). *B. sudanica*, *B. alexandrina* and the Rhodesian, Liberian and Ethiopian populations of *B. pfeifferi* formed a progressive series with respect to the state of the peaks H and G (the only variable factor) (Figs. 1 and 2), and these could therefore be regarded as variations between populations of the same species. On purely morphological grounds, however, members of these populations belong to 3 different species.

Thus, the similarity in electrophoretic patterns may be the result of the uncertain state of the systematics of the genus, which has hitherto been based on differences of conchological and anatomical features which have proved unsatisfactory, as pointed out by Mandahl-Barth (1958). Wium-Andersen (1973) was able to confirm the morphological characters used to identify 4 species of African *Biomphalaria* by recognizing correspondingly different esterase patterns. Malek & File (1971), however, found, working with 9 populations of *B. glabrata*, 2 populations each of *B. tenagophila* and *B. obstructa* and 1 population each of *B. straminea* and *B. peregrina*, that a total of 5 esterase patterns could be recognized. These patterns occurred in varying proportions in the various populations of the 5 different species. It is relevant to refer to the work of Wright (1966), Wright & File (1968) and Davis & Lindsay (1967), which suggest caution to the effect that though esterase patterns can be relied upon to demonstrate population differences within a species, they are not necessarily fool-proof in evaluating relationships between different species, because species analysis could be complicated by significant population differences and sometimes interpopulation differences may even be greater than those between species.

In some cases, minor intrapopulation variations were observed, e.g., in the Toquor River Ethiopian population (Fig. 2), the 2 Tanzanian populations (Fig. 3) and the Kenyan population (Fig. 4). These variations are usually in terms of the relative degree of prominence of certain peaks like H and G in the Arusha, Tanzanian and Kenyan populations. On the other hand, the Rhodesian, Lake Awasa Ethiopian and Liberian populations were uniform. This trend was also observed for *Bulinus* populations by Wright & File (1968).

Finally, both Malek & File (1971) and Wium-Andersen (1973) have inferred a correlation between esterase patterns of populations of *Biomphalaria* spp. from South America and Africa and their susceptibility to *Schistosoma mansoni* infection. Unfortunately, time did not permit the investigation of this aspect in the present study. A useful experiment in a laboratory like the Museum of Zoology, The University of Michigan, where there are cultures of many populations of snails, would

be to challenge individuals of the various populations of *Biomphalaria* with different strains of *S. mansoni* and to determine their susceptibility. Then the foot muscle esterase pattern could be determined for each snail. It would then be possible to verify directly the actual relationship between susceptibility to infection and esterase patterns in *Biomphalaria* spp. populations.

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IMMUNOLOGICAL RELATIONSHIPS OF TWO SPECIES OF LYMNAEIDAE (MOLLUSCA: BASOMMATOPHORA) FROM MACEDONIA, YUGOSLAVIA[1]

J. B. Burch and S. Hadžišče

ABSTRACT

Immuno-taxonomic studies of *Radix relicta* of Lake Ohrid and *Radix* sp. in one of its feeder-springs at the southern end of the lake (at St. Naum) show, by their "identity" reaction, that they are clearly related to *R. auricularia* and, by inference from previous immunological comparisons of *R. auricularia* with various other *Radix* spp., to radicine lymnaeid species in general. "Non-identity" reactions occurred when antigens from the Ohrid species were tested with antisera from species representing other lymnaeid species-groups (*Austropeplea, Bulimnea, Fossaria, Lymnaea, Pseudosuccinea* and *Stagnicola*). The findings in regard to *Radix* bear out recent studies, which indicate that distinct "species-groups" (i. e., taxonomic units usually referred to as "genera" or "sub-genera") do indeed occur in the Lymnaeidae and that immunological data correlate well with previous morphological information (and, in the case of *Radix*, with cytology).

The Lymnaeidae are one of the most common and wide-spread of all animal groups, species being found in the freshwaters of all the major land masses of the world. Many species and genera have been named, but few malacologists seem to agree on their taxonomy. This is hardly surprising since there is a dearth of critical scientific information on which to build solid systematic concepts. We have little information on genetics and almost no data on breeding potential or reproductive isolation for any of the nominal species, and for no species have the morphological parameters been adequately defined in terms of modern biological concepts.

In an effort to gather more systematic data of particular significance for understanding the relationships of the various taxonomic units within the family, we have been using various methods, including classical conchology and breeding studies. One approach that has been specially illuminating is immunology of proteins: our techniques are designed to show whether or not various related species have developed immunologically detectable differences in foot muscle proteins during their evolutionary divergence. Species from widely separated regions, such as northern and central Europe, Japan, India, South Africa, U.S.A., etc., have already been cross-tested. In the present report, 2 species of Macedonian *Radix*, one solely endemic in ancient Lake Ohrid, another occurring in a feeder-spring of that lake, have been tested against another species of *Radix* (imported into the U.S.A.) and various other lymnaeids from North America and Australasia.

METHODS AND MATERIALS

The immunological procedures used were as follows: antibodies against snail antigens were produced in virgin female rabbits by 2 consecutive series of 5 1-ml injections of homogenized

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snail foot muscle tissue in increasing concentrations. The antigen injections consisted of the supernatant liquid obtained after centrifugation of the homogenized snail foot tissue. The resulting rabbit serum containing the antibodies was sterilized by filtration, after which an anti-bacterial agent (merthiolate, i.e., sodium-ethylmercurithiosalicylate; 0.001%) was added. Micro-Ouchterlony plates for the double diffusion test were prepared by fastening a glass ring, 21 mm in inside diameter and 10 mm in height, to a microscope slide. The semi-solid medium used to fill the rings to about 5 mm was a 1% agar gel with 0.4% NaCl and 0.0001% merthiolate.

Four wells were cut in the gel and filled with antigens or antiserum from the 2 species to be tested against one another according to the scheme illustrated in Fig. 1. Full-strength antisera were used. The fluid containing the antigen was the supernatant obtained from centrifuging 0.1 g snail foot tissue homogenized in 1.0 ml snail physiological saline. Proteins occurring in one species but not in the other could be observed by the precipitin reaction of diffusing protein fractions between wells 1 and 4, because the antiserum in well 4 had to pass through a surrounding barrier of preabsorbed heterologous antigen, allowing only those antibodies through to react with antigens from well 1 that were not common to the 2 populations. Thus, we could determine whether or not the 2 species in question had detectably diverged in their foot muscle proteins during their evolution. (Differences between homologous and heterologous extracts can be seen by comparing the precipitin reactions between wells 1 and 2 and between wells 2 and 3, respectively. The space between wells 3 and 4 serves as a control to indicate when the system is overloaded with antigen or antibody.) Therefore, the presence ("non-identity") or absence ("identity") of precipitin bands between wells 1 and 4 were of prime interest to us. For greater detail of these techniques see Burch & Lindsay (1970).

Antibodies were produced against the 8 species of Lymnaeidae (7 genera) listed below:

Austropeplea ollula (Gould). Watercress farm near Pearl Harbor, Oahu, Hawaii. Introduced from Japan.

Bulimnea megasoma (Say). Roadside drainage ditch, highway M-55, about 2 miles west of Houghton Lake, Roscommon County, Michigan, U.S.A.

Fossaria obrussa (Say). From the bank of the Kalamazoo River at the recreation park of the town of Comstock, Section 19, Comstock Township, Kalamazoo County, Michigan, U.S.A.

Lymnaea stagnalis appressa Say. Au Sable River, 1/2 mile southwest of Grayling, highway M-72, Crawford County, Michigan, U.S.A.

Pseudosuccinea columella (Say). Drainage ditch to Bass Lake, Section 28, Hamburg Township, Oakland County, Michigan, U.S.A.

Radix auricularia (Linnaeus). Trenton Channel of the Detroit River, Grosse Ile, Wayne County, Michigan, U.S.A. Introduced from Europe.

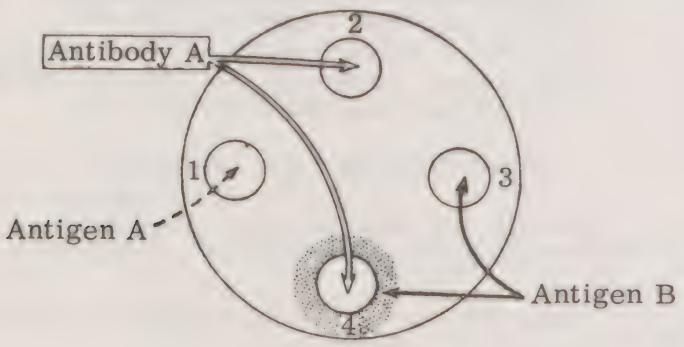

FIG. 1. Procedure for filling the wells with antigens and antisera in the micro-Ouchterlony double diffusion agar gel tests. Preabsorbed antigen is around well 4. Excess antigen for the preabsorption was removed before antiserum was placed in well 4.

Stagnicola elodes (Say). From a pond formed by an old abandoned mill stream formerly flowing into the Huron River, Section 11, Scio Township, Washtenaw County, Michigan, U. S. A.

Stagnicola emarginata (Say). Lake Ann, Benzie County, Michigan, U. S. A.

Antigens (i. e., foot muscle homogenates) were made from the following Macedonian species of *Radix*:

Radix relicta Polinski. Lake Ohrid, Macedonia, Yugoslavia (Fig. 2a).

Radix sp. From the pool of a feeder-spring at the southern end of Lake Ohrid at St. Naum, Macedonia, Yugoslavia (Fig. 2b).

FIG. 2. Shells of Ohrid *Radix*. a, *R. relicta* Polinski from Lake Ohrid. b, *Radix* sp. from spring at St. Naum. Scale marked in mm.

RESULTS

TABLE 1. Precipitin reactions between Ohrid lymnaeid antigens and various lymnaeid antisera.

Antisera	Antigens	
	Radix relicta (Lake Ohrid)	*Radix* sp. (St. Naum)
Austropeplea ollula	+	+
Bulimnea megasoma	+	+
Fossaria obrussa	+	+
Lymnaea stagnalis appressa	+	+
Pseudosuccinea columella	+	+
Radix auricularia	0	0
Stagnicola elodes	+	+
Stagnicola emarginata	+	+

+ = "non-identity" reaction; 0 = "identity" reaction.

The precipitin reactions in regard to immunological "identity" or "non-identity" of the 2 Macedonian *Radix* populations with the various lymnaeid antisera are shown in Table 1. Non-identity reactions occurred with all of the antisera tested, except for the antiserum of *Radix auricularia*. With the latter species, both Ohrid populations showed complete immunological correspondence, indicating that the phylogenetic divergence of *R. auricularia* and the Ohrid species has not yet proceeded to a stage where new kinds of foot muscle proteins have evolved. However, foot muscle proteins that do not occur in the Ohrid species (i.e., in *Radix*) are present in all of the other lymnaeids tested. Figs. 3 and 4 show photographs of micro-Ouchterlony plates of some of the precipitin reactions. The greatest number of "non-identity" precipitin bands occurred in the tests with *Lymnaea stagnalis* (Figs. 3c, 4c). The greatest dissimilarity of Ohrid species' antigens to the various antisera was observed with *Austropeplea ollula* and *Fossaria obrussa* (Figs. 3a,b; 4b).

DISCUSSION

In 1929, Polinski described from ancient Lake Ohrid, which has existed since the Pliocene and has a distinctive endemic freshwater fauna, a lymnaeid mollusk which he named *Radix relicta*. It is the only species of the world-wide family Lymnaeidae that occurs in the lake, although other species are found in aquatic habitats in the general area (e.g., species such as *Lymnaea stagnalis*, *Stagnicola "palustris"* and *Fossaria truncatula*). A population of *Radix* rather distinct from *R. relicta*, and as yet of undetermined taxonomic status, is found in the cold spring pool at St. Naum, which flows into the lake at its southern end.

The genus *Radix* to which *R. relicta* was assigned by Polinski is an extremely interesting one, and one that has previously (Burch, 1965) been speculated to represent perhaps the most ancient living lymnaeid stock (except for the Australasian *Austropeplea*; see Burch, 1967; Inaba, 1969). Because of this, it was of more than passing interest to us to test the immunological reactions of antigens of the 2 Ohrid populations to antisera of representatives of some of the major species-groups currently found throughout much of the rest of the world.

The family Lymnaeidae has been divided in the past into a number of species-groups (i.e., genera or subgenera), which generally can be recognized by their distinctive shell features. Nevertheless, lymnaeids have caused taxonomists much difficulty in the past, and there often has been little agreement as to which species constitute a generic or subgeneric group or as to the nomenclature that would apply to such species-groups. Hubendick (1951) has argued against the validity and recognition altogether of generic or subgeneric taxa within the Lymnaeidae (except for recognizing the very aberrant limpet-like *Lanx* as being distinct from *Lymnaea*). However, we have found that the family Lymnaeidae comprises a number of immunologically distinct species-groups, and that these groups correspond to the main, classically recognized genera (e.g., *Lymnaea* s.s., *Stagnicola*, *Fossaria* (=*Galba*), *Radix*, etc.) (Burch & Lindsay, 1973). Because of these immunological characteristics, serological methods such as ours are ideal to determine the systematic relationships of species of doubtful taxonomic placement (e.g., see Burch, Lindsay & LoVerde, 1971; Burch & Lindsay, 1972). Although we now have established the broad framework of immuno-taxonomy in the Lymnaeidae, the information available so far provides only the bare skeleton, and further details in regard to many species of lymnaeids of doubtful systematic placement throughout the world need to be provided.

The Ohrid Lymnaeidae fit into the lymnaeid immunological scheme as radicine species, as one might have expected from Polinski's taxonomic placement (on the

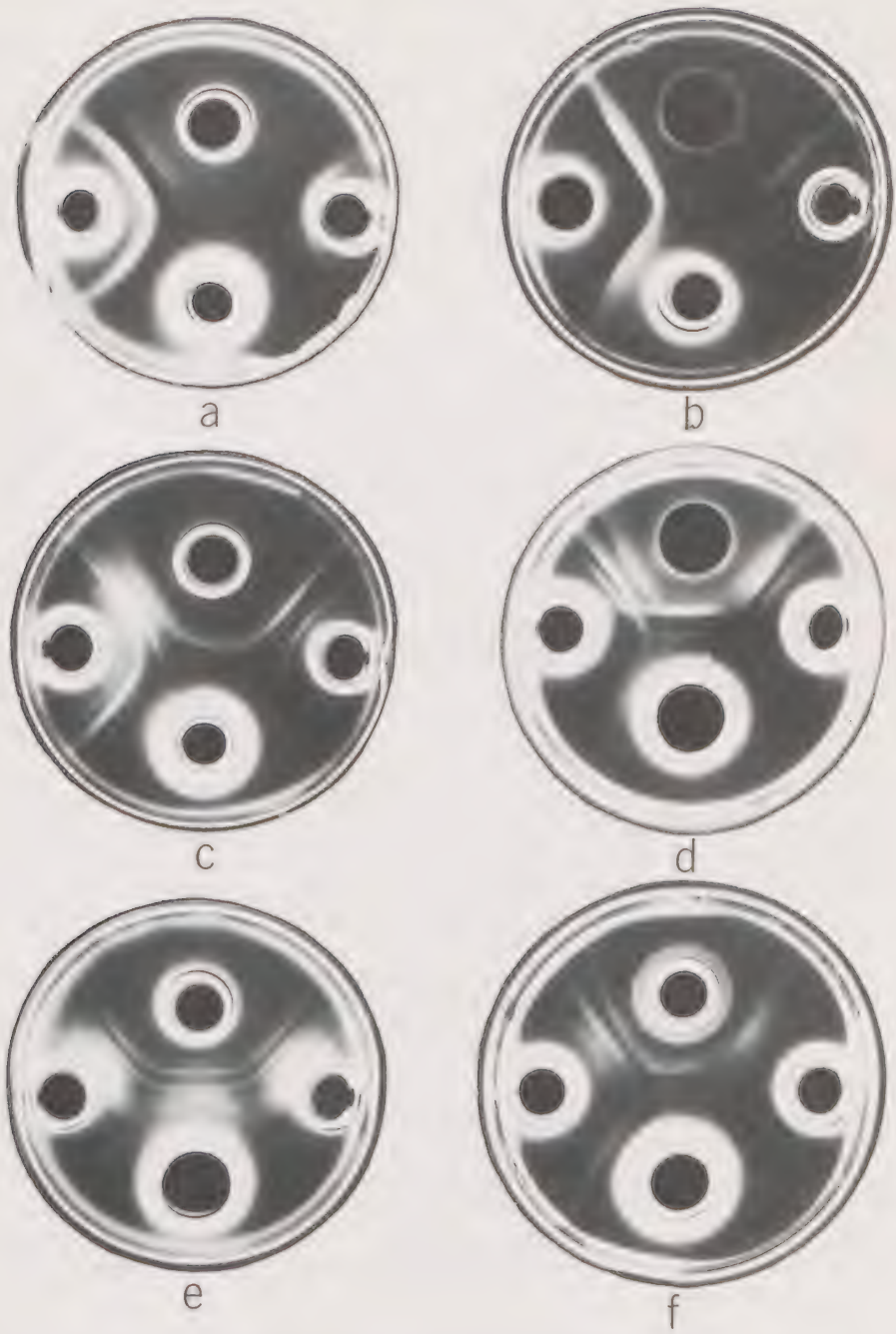

FIG. 3. Agar gel diffusion plates of *Radix relicta* antigen tested against various lymnaeid antisera. a, *Austropeplea ollula*. b, *Fossaria obrussa*. c, *Lymnaea stagnalis appressa*. d, *Pseudosuccinea columella*. e, *Radix auricularia*. f, *Stagnicola elodes*. In each case the preabsorbed well is at the bottom (see Fig. 1). "Non-identity" precipitin reactions occur in the agar between the left and bottom wells in each case, except for *R. auricularia* (Fig. 3e).

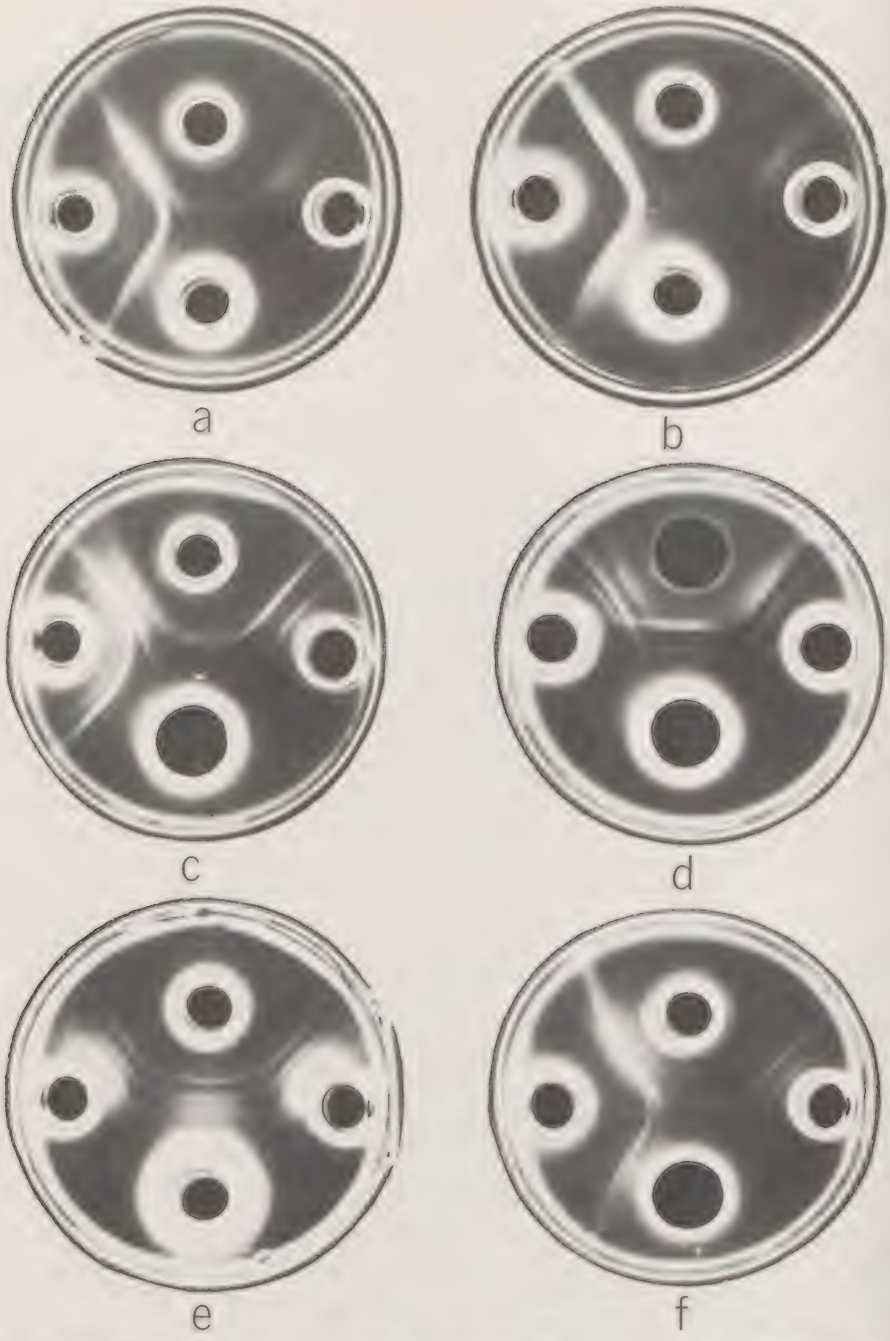

FIG. 4. Agar gel diffusion plates of *Radix* sp. (St. Naum) antigen tested against various lymnaeid antisera. a, *Bulimnea megasoma*. b, *Fossaria obrussa*. c, *Lymnaea stagnalis appressa*. d, *Pseudosuccinea columella*. e, *Radix auricularia*. f, *Stagnicola emarginata*. In each case the preabsorbed well is at the bottom (see Fig. 1). "Non-identity" precipitin reactions occur in the agar between the left and bottom wells in each case, except for *R. auricularia* (Fig. 4e).

basis of shell characters) of *Radix relicta* and from the seemingly obvious relationship of that species to the population at St. Naum. Nevertheless, the radicine affinities of Ohrid Lymnaeidae were not necessarily predictable prior to our studies, if one assumes (e.g., see Walter, 1969) that lymnaeid shells are subject to considerable convergent evolution and that, hence, their characters would not be especially good for indicating phylogenetic relationships.

Radix auricularia does not have any immunologically detectable foot muscle proteins that are not also found in the Ohrid lymnaeids, indicating that *R. auricularia* has apparently not evolved different foot muscle proteins in the evolutionary divergence which led to the separation of the 3 species. We could not determine if the Ohrid species have foot muscle proteins not found in *R. auricularia*, since we did not have enough material to produce antisera for either of the 2 Ohrid populations. However, if the Ohrid species have been evolutionarily stable for a long period of time due to their protected habitat and stable environment, then one would not expect them to have evolved in that respect.

The fact that no immunologically detectable proteins occurred in *Radix auricularia* that did not also occur in the 2 Ohrid populations does not mean that *R. auricularia* and the Ohrid species are conspecific. The evolution of foot muscle proteins in lymnaeids as far as known seems to always have occurred with a major taxonomic divergence and not with speciation within the species-group. [For example, *R. auricularia* collected in North America is indistinguishable from the Indian *R. luteola* by our immunological methods, although morphologically the 2 species are quite distinct (Burch & LoVerde, 1973). Similarly, the North American *Stagnicola elodes* and *S. emarginata* show complete immunological correspondence of foot muscle tissues although the 2 species are clearly reproductively isolated (Burch & Ayers, 1973).]

Although most of the antisera were produced to snails from North America, we have previously shown that "identity" reactions, i.e., complete immunological correspondence, occur over a very wide geographic range if the species in question are closely related. For example, "non-identity" reactions do not occur between *Lymnaea stagnalis appressa* (Michigan, U.S.A.) antiserum and *L. stagnalis* (Poland) antigen, or between *Stagnicola elodes* (Michigan, U.S.A.) antiserum and *S. corvus* (Poland) antigen, or between *Radix auricularia* (Michigan, U.S.A. [introduced]) antiserum and antigens of other radicine species, such as *R. peregra* (England), *R. natalensis* (Africa) and *R. luteola* (India), or between *Fossaria obrussa* (Michigan, U.S.A.) antiserum and *F. truncatula* (Austria) antigen (see Burch & Lindsay, 1968; Burch, Lindsay & LoVerde, 1971; Burch & LoVerde, 1973; LoVerde & Burch, 1973).

Whether *Radix relicta* of Lake Ohrid and *Radix* sp. of the feeder-spring at St. Naum are relict species, having lived in the ancient lake and spring for an exceptionally long time, or whether they are derived from more recent immigrants, is not yet known. The present study gives no direct information bearing on that question. Hubendick (1951) considered *R. relicta* to be conspecific with *R. peregra*. However, no careful morphological study has been done comparing these 2 nominal species.

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BRIEF COMMUNICATIONS

A REVIEW OF SOME LAND SNAILS OF THE EASTERN UNITED STATES. — During the summer of 1973, I visited the Academy of Natural Sciences of Philadelphia (ANSP), the National Museum of Natural History (USNM) and The University of Michigan Museum of Zoology (UMMZ) to study type specimens and other land snail material in these museums. Examination of these specimens, as well as material in the author's private collection makes it necessary to reduce 25 species and subspecies of eastern United States land snails to synonymy (23 for the first time; 2 others have been discussed previously[1]).

Carychium mexicanum Pilsbry [*Carychium floridanum* Clapp]. The holotype (ANSP) of *C. mexicanum* is a slightly immature shell in which the lip is expanded but not thickened, and is thus a poor specimen for the identification of a species. Other specimens from Mexico and Guatemala identified by H.A. Pilsbry as *C. mexicanum* do not appear to be specifically distinct from *C. floridanum*, having the very thick lip characteristic of that species.

Vertigo rugosula Sterki [*Vertigo wheeleri* Pilsbry]. The holotype (ANSP) of *V. wheeleri* shows an injury to the spire which has caused some distortion of the later whorls. It appears to be only an aberrant *V. rugosula*.

Pseudosuccinea columella (Say) [*Succinea concordialis* Gould]. There were 5 specimens in the original lot (39750) labelled *Succinea concordialis* at USNM. This lot now contains only 4 specimens. If these 4 are paratypes, then the holotype (if ever selected) cannot be found. The 4 specimens are *Pseudosuccinea columella*, and so the name *S. concordialis* must be placed in the synonymy of that species.

Succinea forsheyi Lea [*Succinea wilsoni* Lea; *Succinea witteri* Shimek; *Succinea concordialis* Auct.]. The name *S. forsheyi* must be used for the snail which has been known as *S. concordialis*, with *S. wilsoni* and *S. witteri* as synonyms. The *Succinea* which is found commonly around Lake Concordia, Louisiana, is *S. unicolor* Tryon.

Philomycus venustus Hubricht [*Philomycus bisdosus* Branson]. *Philomycus venustus* is a rather variable species and *P. bisdosus* represents one extreme of that variation.

Philomycus carolinianus (Bosc) [*Philomycus batchi* Branson]. *Philomycus batchi* represents a melanistic color form of *P. carolinianus*.

Pallifera marmorea Pilsbry [*Pallifera hemphilli marmorea* Pilsbry; *Pallifera tornescalis* Branson]. Topotypes of *P. tornescalis* are not distinguishable from *P. marmorea*. *Pallifera marmorea* is a rather common slug in the Ozark Region in Missouri, Arkansas and eastern Oklahoma.

Pallifera fosteri F.C. Baker [*Pallifera megaphalica* Grimm]. There is no difference in the color pattern between *P. fosteri* and *P. megaphalica* and there is no real geographical separation. The genitalia of *P. megaphalica* is larger, but there does not appear to be any structural difference, a difference which one finds between the other species of the genus. The difference in penis size between *P. fosteri* and *P. megaphalica* may be clinal or it may be associated with the generally larger size of Piedmont and Atlantic Coastal Plain specimens. *Pallifera fosteri* occurs from near sea level along the Atlantic and Gulf coasts to over 5000 ft. in the southern Appalachian Mountains.

Punctum smithi Morrison [*Punctum lammellatum* Hubricht]. *Punctum lammellatum* appears distinct from *P. smithi* in its very long lamella and its lighter color. However, it seems to be much too rare to be a valid species, i.e., I found 2 specimens in Kentucky and 4 in Virginia, each time being found associated with *P. smithi*. I now believe it to represent some diseased condition of the latter species.

Discus nigrimontanus (Pilsbry) [*Discus bryanti nigrimontanus* (Pilsbry); *Discus patulus* form *edentulus* Pilsbry; *Discus patulus edentulus* Hubricht]. *Discus patulus edentulus* is more closely related to *D. nigrimontanus* than to *D. patulus* (Deshayes). The small differences between it and *D. nigrimontanus* do not seem to be enough to warrant subspecific recognition. *Discus patulus edentulus* resembles *D. nigrimontanus* with some small introgression from *D. patulus*.

Anguispira alternata (Say) [*Anguispira clarki* Vanatta]. The holotype (ANSP) of *A. clarki* is a dwarf *A. alternata* in which there is an injury to the spire, causing distortion of the later whorls. Mr. J.B. Clark collected normal sized *A. alternata* at the same place.

Anguispira strongylodes (Pfeiffer) [*Anguispira alternata strongylodes* (Pfeiffer); *Anguispira alternata crassa* Walker; *Anguispira alternata macneilli* Walker]. *Anguispira strongylodes* is strongly ribbed in the northern part of its range where it overlaps the range of *A. alternata* (Say), but its ribs become gradually weaker southward, becoming quite weak along the southern border of its range. This southern form has been named *macneilli*. The difference is too clinal for subspecific recognition.

Glyphyalinia wheatleyi (Bland) [*Retinella wheatleyi* (Bland); *Retinella circumstriata* (Taylor); *Glyphyalinia circumstriata* (Taylor)]. Topotypes of *G. circumstriata* from the original lot (ANSP 386340) were examined and found to represent *G. wheatleyi*. There is considerable variation in the spiral striation of *G. wheatleyi*, varying from barely perceptable to quite distinct. Dr. H.B. Baker's studies of *Retinella cumberlandiana* (Clapp) were based on small *G. wheatleyi*. His anatomy and key characters apply to *G. wheatleyi* and not to *G. cumberlandiana*. *Glyphyalinia cumberlandiana* (Clapp) is a very small species with a subhyaline shell shaped like that of *G. raderi* (Dall). The shell of *G. roanensis* (H.B. Baker) looks very much like an immature *G. rhoadsi* (Pilsbry) in shape, but the sculpture is different. There are no shell characters by which *G. wheatleyi* and *G. burringtoni* (Pilsbry) can be distinguished. Whether or not the hook at the end of the penis of *G. burringtoni* is a valid taxonomic character to distinguish it from *G. wheatleyi* is not known. This needs further study.

Glyphyalinia clingmani (Dall) [*Retinella clingmani* (Dall); *Retinella approxima* (Walker & Pilsbry)]. The holotype (ANSP) of *R. approxima* is a specimen of *G. clingmani* in which an injury to the spire has caused considerable distortion to later whorls.

Mesomphix globosus (MacMillan) [*Mesomphix ruidus* Hubricht]. The anatomical differences between *M. globosus* and *M. ruidus* are not constant and there is no geographical separation of the 2 species.

Mesomphix vulgatus H.B. Baker [*Mesomphix derochetus* Hubricht]. The anatomical differences between these 2 species are the differences between specimens relaxed in a Chlorotone solution prior to fixation and specimens which were killed in alcohol without anesthesization.

Paravitrea capsella (Gould) [*Paravitrea placentula* (Shuttleworth); *Paravitrea placentula lithodora* Pilsbry]. The specimens of *P. capsella* at ANSP received from Gould and believed to be paratypes are somewhat immature specimens of the species later described as *P. placentula*.

Mesodon subpalliatus (Pilsbry) [*Mesodon verus* Hubricht]. H.A. Pilsbry placed *M. subpalliatus* in the subgenus *Patera*. However, it belongs in the subgenus *Inflectarius*.

Mesodon mitchellianus (Lea) [*Mesodon burringtoni* Hubricht]. My first specimens of *M. burringtoni* were rather depauperate and seemed closer to *M. downieanus* (Bland) than to any other species. Since its description, much more material has been collected, most of it with larger shells, which are not distinguishable from those of *M. mitchellianus*. It has also been found at 2 places in West Virginia along the New-Kanawha River system. The original home of *M. mitchellianus* was in southwestern Virginia, from where it was washed down the New-Kanawha River system to spread out across Ohio and adjoining states.

Stenotrema hirsutum (Say) [*Stenotrema burringtoni* Grimm]. I can find no character by which topotypes of *S. burringtoni* can be distinguished from *S. hirsutum*.

Stenotrema labrosum (Bland) [*Stenotrema glassi* Branson]. The holotype (ANSP) of *S. glassi* is a specimen of *S. labrosum* without a lip notch. The specimen shows an injury to the shell behind the lip.

Polygyra texasiana (Moricand) [*Polygyra rexroadensis* Taylor]. The development of spiral sculpture in *P. texasiana* is quite variable. In some lots it is not present; in others it may be well developed. The holotype (UMMZ) of *P. rexroadensis* is slightly immature which accounts for the apertural differences.

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(1) *Nautilus*, 1960, 74: 82; *Sterkiana*, 1965, 32: 4.

OVIPOSITION IN THE LAND SNAIL *ANGUISPIRA ALTERNATA* (STYLOMMATOPHORA: ENDODONTIDAE). — During an investigation of the reproductive biology of the land pulmonate snail *Anguispira alternata* (Say), a series of photographs were taken to record the actual process of egg deposition. Since this process has been seldom documented in the literature for any land snail, it is presented here.

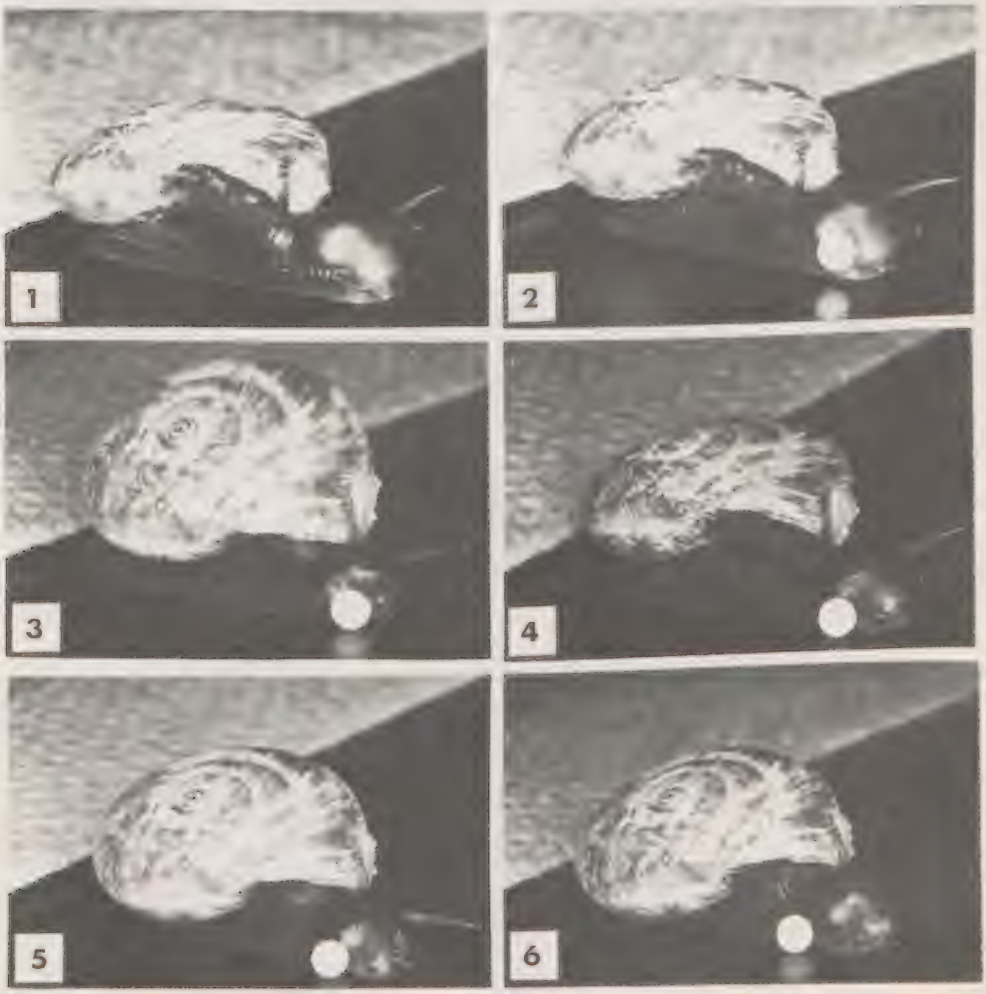
Each egg is released individually at approximately 20 minute intervals, and the snail may lay as many as 60 eggs in a clutch. The opening of the genital pore is usually not visible except when distended by the emerging egg. The egg initially adheres to the everted genital atrium (vagina) but is then quickly released in a matter of seconds, after which the atrium slowly withdraws into the body.

The snail normally deposits its eggs just beneath the surface of the soil or under the bark of fallen trees (Fig. 10). However, once the snail has begun to release its eggs, it can be gently interrupted, removed from the soil and placed in a setting which is more appropriate for photography. The use of an electronic flash minimizes the disturbance to the animal.

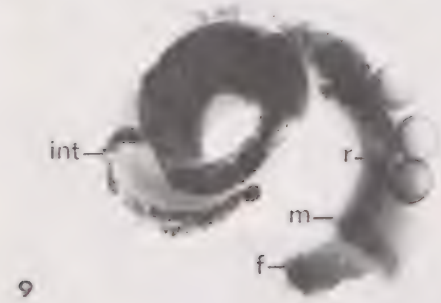
These photographs (Figs. 1-6) were taken at approximately 3 second intervals. This particular animal had already laid 15 eggs, whereupon it was removed from the soil and placed on a black surface and allowed to move freely. The series of consecutive exposures were taken in a total elapsed time of about 18 seconds with a hand held 35-mm camera.

Immediately afterwards, the animal was fixed and dissected. Examination of the "uterus" (spermoviduct) revealed that there were more large eggs, fully formed and ready to be deposited (Figs. 7, 8). Because these eggs have a heavily calcified shell, they are opaque to low energy X-rays (Fig. 9).

The ultrastructure and mineral composition of the calcareous eggs of this and other land snails have been investigated (Tompa, 1973, 1974). Further work in this field is now in progress.



FIGS. 1-6. *Anguispira alternata* in the act of oviposition. See text for details.



FIGS. 7, 8. Dissections of a gravid *Anguispira*, having been fixed immediately after deposition of an egg. Fig. 7 shows the general features of a snail with the shell removed. It shows an enlarged albumen gland (alb), little hermaphroditic duct (lhd), the kidney (k) (the mantle is laid back to expose the kidney), the prostate gland (pr) (white), the eggs inside the spermoviduct (in a single file, with the next egg to be deposited labeled #9). Fig. 8 presents a more detailed view of the eggs and their location in the same animal. Each egg measures about 2.6 mm in diameter.

FIG. 9. Radiograph of another *Anguispira* specimen in a similar condition. The shell has been removed and part of the mantle removed. The large, radio-opaque eggs are easily seen, though they are still inside the spermoviduct; the mantle edge (m) is visible above the contracted foot (f). The intestine (int) and rectum (r), as well as the rest of the digestive tract, contain particulate matter such as soil and sand grains from normal feeding activity. Each egg measures about 2.6 mm in diameter.

FIG. 10. A single clutch of *Anguispira* eggs laid in the soil.

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A COLCHICINE HYPOTONIC SQUASH TECHNIQUE FOR CHROMOSOME SPREADS OF PULMONATE LAND SNAILS. — Chromosome studies have gained an increasing importance in the understanding of the taxonomy and phylogeny of various molluscan taxa (Burch, 1961). Burch (1962, 1965a, 1965b) has used cytotaxonomic analyses of certain mollusks to show evolutionary relationships. The majority of reports on molluscan chromosomes, however, deal mainly with the determination of chromosome numbers, and only a few investigations have attempted the more difficult problem of karyotype analysis (Patterson, 1969, 1971). One reason for the scarcity of such reports is the difficulty of obtaining good chromosome spreads which can be used for karyotyping.

Burch (1968) described a technique for obtaining spreads of chromosomes in metaphase in which he utilized a tissue culture of pulmonate land snail ovotestes in a medium with colchicine. The success of this technique, however, requires relatively complex and elaborate equipment and facilities. Longwell *et al.* (1967) worked with oyster embryos in a sea water and colchicine medium. Patterson (1971) described a technique using embryos of freshwater snails which were treated with an isotonic Velban solution and followed by hypotonic NaCl. Dolph & Humphrey (1970) injected the chiton *Katherina tunicata* with colchicine and subsequently subjected digestive gland tissue to aspiration, centrifugation, smearing, air drying and staining; this technique provided chromosomes in mitotic metaphase. This communication is a description of an easy and inexpensive technique for obtaining clear, distinct chromosome spreads of land snails which lend themselves readily to karyotype analysis.

The technique which was successfully used is described as follows. Living specimens of *Ashmunella chiricahuana* (Dall 1895) and *A. proxima* Pilsbry 1905 (Polygyridae) were collected from a rock slide below Cave Creek Falls in the Chiricahua Mountains, Cochise County, Arizona, in May 1971. The specimens were brought to the laboratory, fed with lettuce in terraria for 2 weeks, and then allowed to estivate for 1 week. The weight of live snails with shells was determined by a torsion balance. A small window in the 2nd or 3rd whorl of the shell was made with the help of a dissecting needle to allow a syringe needle into the body mass of the snail. The snails were injected with 0.1 ml of 10^{-3}M colchicine per gram of body weight (including the shell) using glass pack B-D 26G 3/8 1/2 cc syringe (by Becton, Dickinson & Co., New Jersey, U.S.A.). The injected snails were kept in finger bowls with moistened paper towels for 6-8 hours; a watch glass covered each finger bowl. The shell of the living animal was broken with the help of forceps and the ovotestes were dissected out in a waxed petri dish under a binocular microscope. Dissection was performed in a 0.65% sodium citrate solution in distilled water and enough 10^{-3}M colchicine solution was added to make a concentration in the medium of approximately 10^{-4}M. After dissection, the ovotestes of the snail were transferred to a solution of 0.65% sodium citrate and 10^{-4}M colchicine in distilled water. The ovotestes were then broken into pieces of about 1-2 mm in length by means of fine forceps. The tissue was kept in hypotonic citrate for 12-15 minutes. After hypotonic treatment, the pieces of tissue were gathered on a clean glass slide with the help of a medicine dropper and the excess hypotonic medium was removed by tilting the slide slightly. The tissue was then fixed in Newcomer's (1953) fluid. Minimum time for fixation in labelled screw cap vials was 36-48 hours. Before staining, the tissue was removed from the fixative

FIG. 1. Mitotic metaphase chromosomes of *Ashmunella chiricahuana*.

and placed in 45% acetic acid for 4 minutes in order to remove the fixative from the tissue; this also provided some hydrolysis. The tissue was stained in bulk either in lactic acetic orcein (Cooperrider & Morrison, 1967), lactic propionic orcein (Dyer, 1963) or Sudan Black B (Bunker, 1961; O.G. Ward, unpubl.). The amount of the stain should be sufficient to cover the tissue completely and more stain should be added if necessary. Each piece of tissue was placed on a pre-cleaned slide with a small drop of stain and macerated with a pair of japanned insect pins (No. 0). The slide was then covered with a pre-cleaned 22x22 mm cover slip. The completed slide was placed between 2 sheets of bibulous paper with the cover slip on the bottom. It was first pressed slowly to remove the excess stain, then full pressure was applied. Care should be taken that no lateral movements of the slide or cover slip are allowed; otherwise the tissue spread will become clumped rendering it unsuitable for cytological studies. The slides can be kept for 6 weeks or more in the freezer of a refrigerator at temperatures below 0°C. Permanent mounts can be made by using any standard procedure. Fig. 1 shows the mitotic metaphase chromosomes of *Ashmunella chiricahuana*. The haploid number was determined to be n=29. We are indebted to Dr. O. G. Ward for his suggestions and assistance.

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1973

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MOLLUSK SEMINAR

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Ann Arbor, Michigan
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24, 25 August 1973

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PROGRAM

Opening remarks, J. B. BURCH

Systematics, Variation and Zoogeography

Convener, James N. CATHER

A review of the *Lampsilis radiata* (Gmelin, 1791) complex in North America (Mollusca: Bivalvia: Unionidae). David H. STANSBERY

Anatomical systematics of freshwater mussels. William H. HEARD

Comparative reproduction in viviparid snails. Virginia A. VAIL

Studies on Physidae (Pulmonata: Basommatophora). I. Penial complex morphological groupings. George A. TE

Scanning electron microscope studies of the embryonic shell surface sculpture in *Bulimus*. C. M. PATTERSON

Freshwater mollusks of Lake Ohrid, Macedonia. S. HADŽIŠČE, J. B. BURCH and C. M. PATTERSON

Growth, Development, Behavior, Physiology and Biochemistry

Convener, C. M. PATTERSON

Effects of various kinds of algae, aquaria, muds and mud extracts, and synthetic muds on the growth of *Biomphalaria pfeifferi*. Y. S. LIANG

Life table parameters of an experimental population of *Omalonyx felina* (Pulmonata: Succineidae). Amy L. SHRADER

Embryological development in *Dentalium*. James N. CATHER

The structure, ciliation and function of the lips of bivalves. T. H. J. GILMOUR

The structure of calcareous snail eggs. Alex S. TOMPA

Behavior responses of *Biomphalaria glabrata*. William A. SODEMAN

Behavioral and physiological studies on locomotion in the giant garden slug, *Limax maximus*. David J. PRIOR and Alan GELPERIN

Comparative aspects of the morphology and physiology of a single identifiable neuron in *Helix aspersa, Limax maximus* and *Ariolimax californica*. David SENSEMAN and Alan GELPERIN

The histochemical identification of galactogen in the Succineidae. Paul H. RUDOLPH

Organ culture of *Helix pomatia* albumen gland in a defined medium. Esther M. GOUDSMIT and Shelley L. FELDMAN

Snails as Intermediate Hosts of Parasites

Convener, William H. HEARD

A simple biochemical method for discerning between diploid and polyploid species of the *Bulinus* (*Isidora*) complex. G. K. LINDSAY

The genus *Bulinus* and schistosomiasis in North Africa. Philip T. LoVERDE

Biology and control of *Bulinus truncatus* in Egypt. Emile S. DEMIAN and Erian G. KAMEL

Experimental infection of *Bulinus sericinus* with *Schistosoma haematobium*. S.-K. WU and J. B. BURCH

The larval interaction of *Paragonimus ohirai* and *Schistosoma japonicum* in *Oncomelania*. Philip T. LoVERDE and Marilyn PARKER

ANATOMICAL SYSTEMATICS OF FRESHWATER MUSSELS

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Abstract

Numerous conchological classifications of freshwater mussels [the Mutelacea ("Etheriidae," Mutelidae and Mycetopodidae) and Unionacea (Amblemidae, Hyrridae, Margaritiferidae and Unionidae)] have been promulgated over the past 150 years, yet only Modell (1942, *Arch. Molluskenk.*, 74: 161-191; 1949, *Ibid.*, 78: 29-48; 1964, *Ibid.*, 93: 71-126) suggested phylogenies based on shell features.

Aside from Simpson's (1900, *Proc. U.S. natn. Mus.*, 22: 501-1044) frequently erroneous accounts, inferred from similar shells of different nominal taxa, Ortmann (1910, *Nautilus*, 23: 114-120; 1911, *Ibid.*, 24: 103-108, 114-120, 127-131, pls. 6-7; 1912, *Ann. Carnegie Mus.*, 8: 222-365, pls. 18-20; 1921, *Mem. Carnegie Mus.*, 8: 451-668, pls. 34-48) presented the first, consistent anatomical groupings of freshwater mussels. He considered that species and genera should be defined by shell characters, but that higher taxa should be delineated by soft-part anatomy, larval aspects and duration of incubation. Ortmann's approach was extended and partially revised by Parodiz & Bonetto (1963, *Malacologia*, 1: 179-213) and Heard & Guckert (1970, *Ibid.*, 10: 333-355), and several animal phylogenies were proposed.

As noted by Heard & Guckert (1970, *op. cit.*), shell features are typically not correlated with animal characters, and the use of 1 set of criteria demonstrates extensive parallelism and/or convergence in the other. Recent availability of many anesthetized, fixed and preserved mussels from southeastern Asia and Africa has made possible a more critical analysis of animal features, and the findings indicate that more conservative characters may be associated with reproduction. This report summarizes a provisional scheme of relationships according to the variations found in the marsupial demibranchs. The genera cited are examples only and do not constitute a complete list of taxa showing specific conditions.

The most primitive marsupial condition is that of an irregular patchwork of discontinuous interlamellar connections in the tetragenous (all 4 demibranchs marsupial) Margaritiferidae (*Cumberlandia*, *Margaritifera*); a partial organization occurs in an oblique orientation of some of the connections in the middle of the demibranchs. Derived from that state, and present in the most primitive (*Gonidea*, *Megalonaias*, *Pilsbryoconcha*, *Pseudodon*) and in the more advanced (*Caelatura*, *Ensidens*, *Scabies*) Amblemidae, is one of vertically-oriented septa that are interrupted by perforations. This condition is also found in the endobranchous (only the inner 2 demibranchs marsupial) Hyriidae (*Castalia*, *Diplodon*, *Hyria*, *Hyridella*, *Prisodon*), primitive endobranchous Mutelidae (*Chelidonopsis arietina*, *Pseudospatha tanganyikensis*), endobranchous "Etheriidae" (*Etheria elliptica*) and in the primitive exobranchous (only the outer 2 demibranchs marsupial) Unionidae (*Cafferia*, *Hyriopsis*, *Physunio*, *Trapezoideus*). The most advanced amblemids (*Amblema*, *Plectomerus*), mutelids (*Aspatharia*, *Mutela*) and unionids (*Anodonta*, *Elliptio*, *Pleurobema*, *Unio*), as well as all investigated endobranchous mycetopodids (*Anodontites*, *Leila*, *Mycetopoda*), were derived by the fusion of the perforations. Furthermore, advanced groups of amblemids, mutelids, mycetopodids and unionids also evolved imperforate non-marsupial septa.

In addition to the change in number and location of the marsupia, and in the closure of the perforations in the marsupial and non-marsupial septa, there evolved a dimorphic spacing of the septa in unionaceans. Males, females and hermaphrodites of the most primitive Amblemidae are morphologically indistinguishable (as are margaritiferids) and can be identified only by examining the gonads; all 4 demibranchs in each sex possess perforated septa that are distantly-spaced. However, a dimorphism occurs in presumably all Hyriidae, advanced Amblemidae and all known Unionidae: the non-marsupial demibranchs (all 4 in males and some hermaphrodites, and 0 or 2 in females and some hermaphrodites) and non-marsupial parts of marsupial demibranchs retain distant septa (about 15 filaments between successive septa), whereas the marsupial septa are densely-spaced (about 3 filaments between successive septa). This condition apparently arose by the evolution of additional septa in the marsupia, at first relatively short (still evident) and subsequently increasing in height. In those groups displaying this dimorphism, it is usually possible (except for hermaphrodites) to determine the sex of an individual without examining the gonads. Inadequate information is available about the mutelacean septal spacing in "etheriids" and primitive mutelids, but the most advanced mutelids and all investigated mycetopodids, many of which are hermaphroditic, have distantly-spaced septa in all 4 demibranchs of all individuals.

If marsupial anatomy is used to delineate subfamilial taxa, one finds that each such group possesses both tachytictic (short-term, only in the Nearctic summer) and bradytictic (long-term, except in the Nearctic summer) incubation periods. For example, among the primitive amblemids with perforated, distantly-spaced marsupial and non-marsupial septa, *Gonidea*, *Pilsbryoconcha* and *Pseudodon* are tachytictic, whereas *Megalonaias* is bradytictic. The duration of incubation may thus be best employed, at least for convenience of communication, in a tribal concept.

Various familial-group and even some generic-group mussels with perforated marsupial septa and a common period of incubation display several kinds of beak sculpture as well as different forms of hinge dentition. Consequently, attempts to analyze fossil shell material present severe difficulties in interpreting phylogenetic affinities, and also zoogeographic relationships. Nevertheless, the animal approach emphasized here shows some distributional patterns.

Margaritiferids, the most primitive mussels, are Holarctic in occurrence and are interpreted as phylogenetic relicts with a contracted range. The most primitive amblemids and unionids range from southeastern Asia to Africa, with a few biogeographical and phylogenetic relicts occurring in North America; the most advanced amblemids and unionids are found in the Nearctic and Palearctic regions. The known hyriids, all presumably comparatively primitive, live in the Australian and Neotropical regions. In the Mutelacea, the very poorly known Recent "etheriids" comprise 1 monotypic genus each in Africa, India and South America, although this assemblage may constitute a composite of mussels of different groups; mutelids are known only from Africa, and mycetopodids are confined to South and Central America.

The primitive amblemids are considered to have given rise to the Mutelidae and "Etheriidae": *Etheria* in Africa and, by way of the eastern Palearctic, to the advanced amblemids of North America (where *Gonidea* and *Megalonaias* occur as relicts). The primitive unionids presumably also migrated across the Bering land bridge into North America, where they evolved into more advanced groups (*Strophitus* and *Uniomerus* persisting as relicts). The Australian hyriids could also have arisen from the primitive amblemids of the Oriental Region. The South American hyriids may have been derived from Oriental amblemids (or hyriids?) that dispersed over an eastern Palearctic-Nearctic route, or from the Australian hyriids through paleantarctic dispersal or perhaps by continental drift. Somewhat similarly, the Neotropical mycetopodids may have been derived from the African mutelids either by way of Ethiopian-Palearctic-Nearctic-Neotropical connections, continental drift or by paleantarctic dispersal.

COMPARATIVE REPRODUCTION IN VIVIPARID SNAILS

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Abstract

The objective of this study, yet in progress, on viviparid reproductive anatomy and seasonal reproductive cycles is to better delineate generic and specific features, and thus to present a basis for the study of other nominal taxa in the family. These snails are ideal subjects for comparative reproductive studies because they are dioecious, sexually dimorphic with respect to the male right tentacle which serves as the copulatory organ, and ovoviviparous, incubating the developing young in the pallial oviduct. The original information presented here was obtained from northern Florida populations of *Campeloma geniculum* (Conrad), *Lioplax pilsbryi* Walker and *Viviparus georgianus* (Lea).

Reproductive systems. Although other malacologists have previously described viviparid reproductive systems in general, there is confusion concerning the identity and function of accessory organs in both males and females. Detailed comparative information is lacking, and little has been done to evaluate the usefulness of anatomical characters in taxonomic and systematic interpretation.

The male system has the same basic organization in all 3 species: testis, proximal vas deferens, seminal vesicle, distal (=pallial) vas deferens, prostate gland and the penial-tentacular complex. What is here termed the seminal vesicle has previously been called the prostate gland, and what is here termed the prostate gland has been considered to be the distal vas deferens (cf. Baker, 1928, *The Fresh Water Mollusca of Wisconsin, Part* 1, *Gastropoda*, Wisc. Acad. Sci., Arts Lett., Madison, Wisc.; van der Schalie, 1965, *Occ. Pap. Mus. Zool., Univ. Mich.*, (611): 1-15). Differences between the 3 taxa occur in the relative size, location and shape of these 6 organs.

The female system consists of an ovary, proximal oviduct, accessory glands and pallial oviduct (="brood sac"). Again, differences between the 3 taxa occur in the relative size, location and shape of these organs. The identity and specific functions of the accessory glands are unclear. In *Campeloma geniculum* and *Viviparus georgianus*, 2 large glands occur posteriorly and ventrally, respectively, to the brood sac. The larger gland has been identified as the albumen gland (cf. Ankel, 1925, *Senckenbergiana*, 6: 1-12; Baker, 1928, *op. cit.*; Mattox, 1938, *J. Morphol.*, 62: 243-261) and the smaller one as the seminal receptacle or spermatheca (Baker, 1928, *op. cit.*; van der Schalie, 1965, *op. cit.*) or a "shell gland" (Mattox, 1938, *op. cit.*). Histological sections of these 2 glands from *C. geniculum* and *V. georgianus* reveal differences in histological organization, yet presumably mature spermatozoa occur in both glands. In *Lioplax pilsbryi*, only 1 gland is distinct, located at the posterior end of the brood sac. However, the posterior wall of the brood sac appears to be more glandular in nature than in the other 2 species, although histological sections of *L. pilsbryi* females have not yet been made to verify this possibility. In addition, the brood sac in all 3 species appears to have walls that vary in thickness according to different phases of the reproductive cycle. The walls are thick (and glandular?) during incubation of young in early stages of development, but very thin when large shelled developing young are incubating.

Reproductive cycles. Previous life history studies on Nearctic viviparids were conducted by Van Cleave & Altringer (1937, *Amer. Natur.*, 71: 167-184) on *Campeloma rufum* (Haldeman), Medcof (1940, *Can. J. Res.*, 18: 165-172) on *C. tannum*, Mattox, Van Cleave & Chambers (1935, *Amer. Midl. Natur.*, 16: 913-920) on *Lio-*

plax subcarinata occidentalis Pilsbry and by Van Cleave & Lederer (1932, *J. Morphol.*, 53: 499-522) on *Viviparus contectoides* Binney. Those studies were based on large collections of post-birth snails from Illinois (Van Cleave and associates) and Ontario, Canada (Medcof). *Campeloma rufum* has been demonstrated to be parthenogenetic (cf. Mattox, 1937, *Z. Zellforsch. mikrosk. Anat.*, 27: 455-464), and no males have been found in *C. tannum*. *Lioplax subcarinata occidentalis* and *Viviparus contectoides* are dioecious, and it was reported for each that the females live up to 3 years and reach a significantly larger size than the males, which live only about 1 year. For those 2 species, and also *Campeloma rufum*, Van Cleave and associates reported the generation of 1 brood per year, with a single birth period in the spring.

STUDIES ON PHYSIDAE (PULMONATA: BASOMMATOPHORA) I. PENIAL COMPLEX MORPHOLOGICAL GROUPINGS

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Abstract

A total of 601 taxonomic names have been compiled to date on the family Physidae, 520 of which had been attributed to the genus *Physa* and 81 to the genus *Aplexa*. The current state of systematics in this family has been briefly reviewed previously (Te, 1973, *Malacol. Rev.*, 6: 61). The family consists of 2 genera, *Aplexa* and *Physa*, with a generally Holarctic distribution extended to Central and South America.

Of the 601 names compiled, 72 were described from Africa, 124 from the Australian and Pacific regions and 13 from South Asia and Southeast Asia. With the exception of a few, all of these names are now referable to such sinistral pulmonate groups as *Physopsis*, *Pyrgophysa*, *Bulinus* (=*Isidora*), *Isidorella*, *Amerianna*, *Physastra*, *Miratesta*, *Camptoceras* and *Diastropha*. *Plesiophysa*, another *Physa*-like pulmonate, is distributed in the West Indies. The above-mentioned groups are all planorbids, many of which are of medical or veterinary importance. *Pseudisidora* is the only sinistral species of the Lymnaeidae known and is found only in Hawaii.

The remaining 392 names have been described from North America, northern Asia, Europe and Central and South America. *Physa* predominates in the northern hemisphere, while *Aplexa* predominates in Central and South America. A preponderance of Physidae were described from North America, comprising 179 species of *Physa* and 10 species of *Aplexa*.

The groups shown in Fig. 1 contain not only species previously unreported but also morphological groups not featured previously in a comparative manner. The new morphological groups are *Aplexa* s.s., *Stenophysa* and *Physa fontinalis*. *Aplexa* differs from *Physa* in not having an accessory gland on the preputium. This confirms the earlier report by Richards (1964, *op. cit.*) and hereby corrects F.C. Baker's erroneous statements to the contrary (1928, *The fresh water Mollusca of Wisconsin*, Pt. I, Wisc. Geol. & Surv., Bull. 70(1), 507 p [p 471, line 25]). *Physa* shows 3 types of terminal male genitalia, separated on the basis of the nature of the penial sheath. In Type a, the penial sheath has a single glandular part; in Type b, the sheath is divided into 2 parts, the part proximal to the preputium being glandular; and in Type c, there is only a single non-glandular part. Other variations noted are: the non-glandular part of the penial sheath may be either muscular, membranous or tissue-like; the accessory gland varies in color from white or yellow to black; and the retractor muscles' attachments also vary between some species, even within a single group. These provide ample basis for further taxonomic divisions and will be reported later when more studies are done.

Groupings in *Physa* made on gross morphology show good correlation with the general aspects of their shells. Species with blunt and rounded apices show Type a genitalia. Species which are elliptical and have expanded penultimate whorls, as in *P. gyrina* and *P. cubensis*, and those with depressed spires and expanded apertures, as in *P. sayii* and *P. parkeri*, all show Type b genitalia. Species with relatively high pointed spires and narrow apertures, as in *P. acuta* and *P. integra*, show Type c genitalia.

No attempt is made at this stage to speculate on the systematic significance of the above groupings. Worth mentioning, however, are *Physa fontinalis* and *P. acuta*, both with Palearctic distributions and morphological representatives in North America. *Physa skinneri*, which is conchologically related to *P. fontinalis*, also shows anatomical correlation with it. Additionally, "*P. pomilia hendersoni* Clench" is not likely, based on the present study, to be a subspecies of *P. pomilia* Conrad.

Specimens of *Physa aurea*, *P. goodrichi*, *P. inflata* and *P. nicklinii*, collected from their type localities in July and August, 1973, were still true in conchological characters, even after more than 100 years, to their type specimens lodged in museum collections. Topotypes of *P. ancillaria* and *P. globosa* were also collected, but I have not been able to compare them with type specimens.

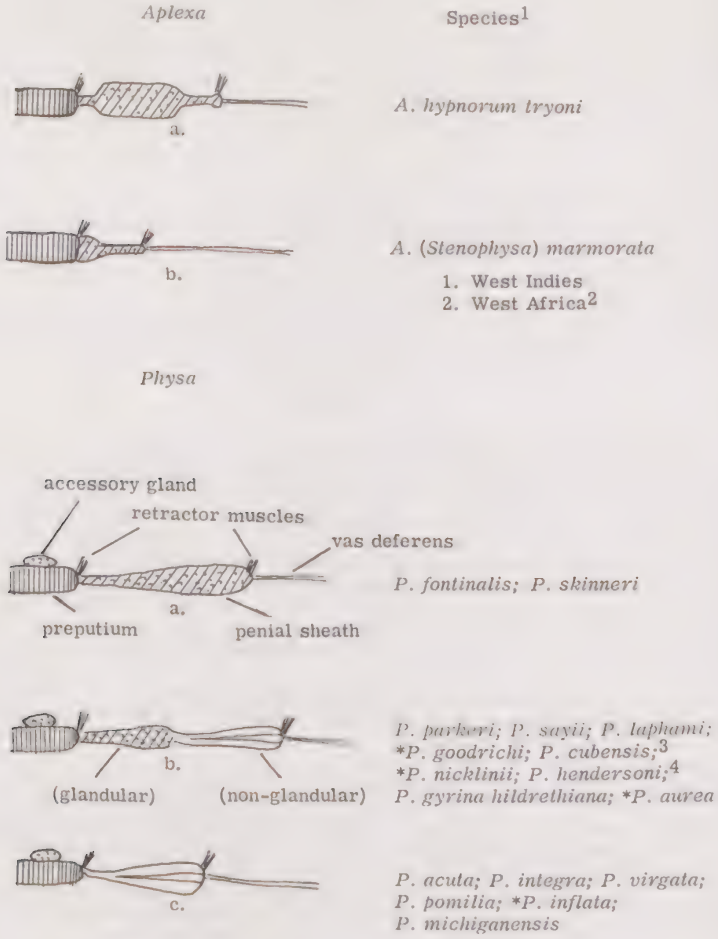

FIG. 1. Physidae penial complex morphological groups, as of 1973. * = topotypes.

[1]Species listed here were all dissected and identified by the author. Identification was based on conchological features, true to museum types, species descriptions and known distributions. Whether or not these are species in the biological sense is not known.

[2]*Aplexa* (*Stenophysa*) *marmorata* from West Africa (Ghana, Nigeria) was probably introduced from the West Indies.

[3]*Physa cubensis* as reported here differs from the illustration given by Richards (1964, *Publ. Hlth. Rep.*, 79(11): 1025-1029). The illustration of shell and penial complex in Richards' paper would assign *P. cubensis* with Type c in the present list.

[4]*Physa hendersoni* Clench was originally described as a subspecies of *P. pomilia* Conrad (Clench, 1925, *Occ. Paps. Mus. Zool., Univ. Mich.*, No. 161, 10 p).

SCANNING ELECTRON MICROSCOPE STUDIES OF THE EMBRYONIC SHELL SURFACE SCULPTURE IN *BULINUS*[1]

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Abstract

Because of its role as an intermediate host for human *Schistosoma haematobium*, the freshwater snail genus *Bulinus* has been studied rather extensively. However, just how many species exist in the genus and how to reliably identify them is not known. Studies are in progress on the embryonic nuclear whorl surface sculpture in the medically important snail genus *Bulinus* using the scanning electron microscope (SEM). The purpose of this study is to denote any sculptural features which may be useful as a basis for species discrimination and which may be indicative of systematic relationships within the genus.

Embryos which were nearly ready to hatch or which were very young post-hatching snails were used. The shells were rinsed in distilled water and affixed to a specimen holder with glue. To avoid charging, the specimens were then coated with gold in a vacuum evaporator prior to examination with the SEM. Observations were made using a JSM-U3 model scanning electron microscope. Photographs were taken using Polaroid Type 55 positive, negative film. Magnifications of 100-600x were routinely used, but shells were also studied at magnifications up to 2000x.

The most prominent features of the embryonic shell are the puncta. The punctational pattern consists of pits in the shell surface which are organized in well defined spiral rows and usually wavy axial rows. The puncta are round to very slightly oblong (Fig. 1) in the subgenera *Isidora* (in *B.* (*I.*) *tropicus*, *B.* (*I.*) *natalensis*, *B.* (*I.*) *truncatus truncatus*, *B.* (*I.*) *truncatus sericinus*, *B.* (*I.*) *hexaploidus* and *B.* (*I.*) *octoploidus*) and *Physopsis* (in *B.* (*P.*) *globosus*), and decidedly elongate in *Bulinus* s.s. (in *B.* (*B.* (=*Pyrgophysa*)) *scalaris*) (Fig. 2). The SEM also reveals in some *Bulinus* (*Isidora*) populations the presence of axial wrinkles (Fig. 3). Axial ribs characteristic of some adult *Bulinus* become evident beginning with the post-embryonic whorl. Puncta become progressively less evident from the younger to the older part of the shell and are usually completely absent beginning with the penultimate whorl. There are differences in the relative density of puncta and variation in the pattern among populations of a species. Because of this variation, it is often difficult to distinguish closely related species on the basis of punctational characteristics. However, each of the subgenera *Isidora*, *Physopsis* and *Bulinus* s.s. (=*Pyrgophysa*) do appear to have distinct punctational characteristics. *Bulinus* (*Physopsis*) differs from *B.* (*Isidora*) in having the puncta situated to one side of a slightly raised ridge or riblet (Fig. 4). As previously noted, the puncta of *Bulinus* s.s. (=*Pyrgophysa*) are distinguished from those of the other 2 groups by being elongate. Hamilton-Atwell & Van Eeden (1971, *Proc. S. Afr. elec. microsc. Soc.*, CSIR Symp. S63: 41-42) also studied shell characteristics of *Bulinus* (*B.* [=*Isidora*]) *tropicus*, *B.* (*P.*) *globosus* and *B.* (*B.* [=*Pyrgophysa*]) *scalaris*) using the SEM. They reported each species to be distinct with regard to shell sculpture but did not infer species group distinction from their results.

There is some evidence of specific differences in the surface sculpture of the initial portion of the nuclear whorl (where puncta are lacking). For example, some forms have prominent spiral wrinkles (Fig. 5), others have a malleated surface (Fig. 6), while still others may be nearly smooth in this region.

Walter (1962, *Malacologia*, 1(1): 115-137) reviewed the literature and studied embryonic shell punctation with the light microscope. He reported microscopic punctation of the embryonic shell to be a universal character in *Bulinus* s.l. He stated that "Differences between punctation of *Bulinus* s.s. [subgenus *Isidora*], *Pyrgophysa* and *Physopsis* were observed but basically the patterns were the same." Information gained from SEM studies now indicate more distinct species group microsculptural differences.

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[1]Supported by grants from the Rockefeller Foundation (GA HS 7411), the Office of International Activities, Smithsonian Institution (SF3-00110), and the U.S. Army Medical Research and Development Command, Office of the Surgeon General, in cooperation with the Commission on Parasitic Diseases of the Armed Forces Epidemiological Board.

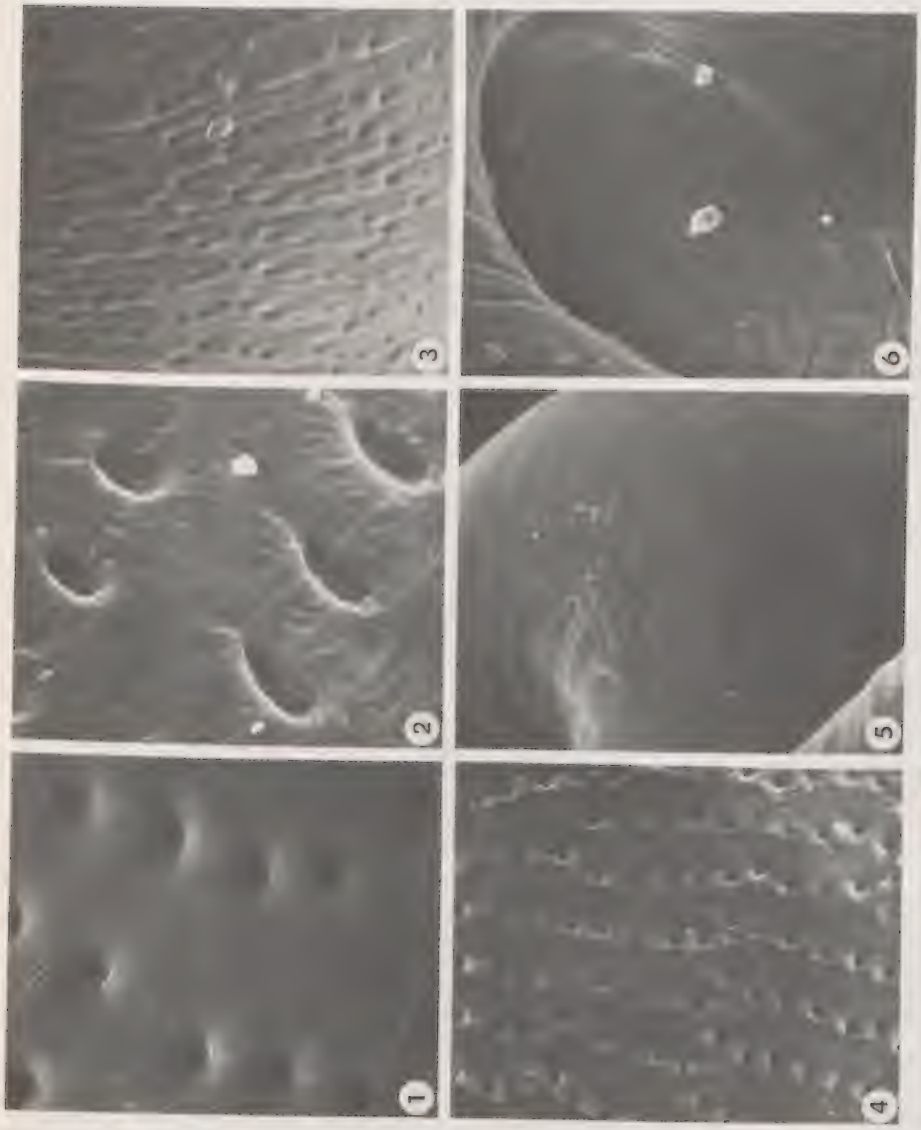

FIG. 1. *Bulinus (Isidora) truncatus scricinus* from Ethiopia, 1272X. FIG. 2. *Bulinus (B. = Pyrgophysa) scalaris* from Rhodesia, 1272X. FIG. 3. *Bulinus (Isidora) tropicus* from South Africa, 384X. FIG. 4. *Bulinus (Physopsis) globosus* from Rhodesia, 384X. FIG. 5. *Bulinus (Isidora) truncatus* from Egypt, 384X. FIG. 6. *Bulinus (Isidora) natalensis* from South Africa, 384X.

FRESHWATER MOLLUSKS OF LAKE OHRID, MACEDONIA[1]

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Abstract

Lake Ohrid is an ancient lake situated in southwestern Europe in the western part of the Balkan Peninsula on the Yugoslav-Albanian border. The lake is located at an altitude of 695 meters, has a surface area of 348 sq. km, a shoreline of 82.5 km, a maximum length of 30.8 km, a maximum width of 14.8 km, and a maximum depth of 286 meters (Stanković, 1960, *The Balkan Lake Ohrid and its living world*, Junk publishers, The Haag, 357 p). Lake Ohrid is a graben lake, having a rather flat bottom and steep sides, especially the sides on the east and west. It is situated in a basin bordered by high mountains, some rising to over 2200 meters. Data regarding the origin, geologic and limnic history of the lake are rather insufficient, but it is believed that the Ohrid basin was formed at the end of the Pliocene, perhaps several million years ago, in the upper reach of an ancient pregrabenian river valley (Cvijić, 1911, *Serb. Acad. Sci.*, spec. ed., Belgrad, p 689-1272).

One of the most prominent elements of the Lake Ohrid fauna are the snails; bivalve species are few. The lake has nearly 70 species of gastropods, about 90% of which are endemic. This is quite a remarkable fauna, comparable to that of other ancient lakes such as Baikal and Tanganyika and ancient rivers such as the Coosa and the Mekong. The more pertinent publications on the mollusk fauna of Lake Ohrid are Brusina, 1896, *C. r. 3rd Congr. internatn. Zool.*, Leiden; Hadžišče, 1955, *C. r. Congr. biol. yougosl. Zagreb*, 1953, p 174-177; Hadžišče, 1956a, *Arch. Hydrobiol.*, 51: 496-499; Hadžišče, 1956b, *Rec. trav. Sta. hydrobiol., Ohrid*, 1: 57-107; Hesse, 1928, *Zool. Jahrb. (allgem. Zool.)*, 45: 1-30; Jaeckel, Klemm & Meise, 1957, *Abh. Berl. Staat. Mus. Tierk. Dresden*, 23: 141-205; Polinski, 1929, *Glas Serb. Acad. sci.*, (137)65: 129-182; Polinski, 1932, *Zool. Jahrb. (Syst.)*, 62: 611-666; Radoman, 1953, *Rec. trav. Sta. hydrobiol., Ohrid*, 1: 63-71; Radoman, 1955a, *Arch. sci., biol., Beograd*, 7: 105-113; Radoman, 1955b, *Rec. trav. Sta. hydrobiol., Ohrid*, 3: 23-39; Radoman, 1955c, *Soc. Serbe biol., Beograd*, ed. spec., 1: 1-106; Stanković & Radoman, 1953, *Rec. trav. Sta. hydrobiol., Ohrid*, 1: 115-122; Stanković & Radoman, 1955, *Arch. sci., biol., Beograd*, 7: 1-20; and Sturany, 1894, *Ann. k. k. natur. hist. Hofmus., Wien*, 9: 369-394.

Malacological investigations are continuing on Lake Ohrid; these include systematics, comparative morphology, chromosome cytology, electrophoresis of foot muscle proteins and immuno-taxonomy. A recent study in our laboratories dealt with the immunological relationships of the Ohrid Lymnaeidae. Immunostudies of *Radix relicta* of Lake Ohrid and *Radix* sp. in a feeder-spring at the southern end of the lake (at St. Naum) show, by their "identity" reaction, that they are clearly related to *R. auricularia* and, by inference from previous immunological comparisons of *R. auricularia* with various other *Radix* spp., to radicine lymnaeid species in general. "Non-identity" reactions occurred when antigens from the Ohrid species were tested with antisera from species representing other lymnaeid species-groups (*Austropeplea*, *Bulimnea*,

a b

FIG. 1. Agar gel diffusion plates, showing the immunological reactions of foot muscle antigens of *Radix relicta* with antisera to (a) *Radix auricularia* and (b) *Lymnaea stagnalis*. Note the non-identity reaction (arrow) to the latter, but lack of such a reaction to *R. auricularia*. A = *Radix auricularia* antigen; Aa = *R. auricularia* antiserum; R = *R. relicta* antigen; S = *Lymnaea stagnalis* antigen; Sa = *L. stagnalis* antiserum.

[1]Supported (in part) by a grant from the Office of International Activities, Smithsonian Institution.

Fossaria, Lymnaea, Pseudosuccinea and *Stagnicola*). The findings in regard to *Radix* bear out recent studies which indicate that distinct "species-groups" (i.e., taxonomic units usually referred to as "genera" or "sub-genera") do indeed occur in the Lymnaeidae and that immunological data correlate well with previous morphological information (and, in the case of *Radix*, with cytology).

LIFE TABLE PARAMETERS OF AN EXPERIMENTAL POPULATION OF *OMALONYX FELINA* (PULMONATA: SUCCINEIDAE)

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Abstract

The tropical slug-like succineid *Omalonyx felina* Guppy occurs naturally in Venezuela and on some islands in the Lesser Antilles. Adults measure 25 to 35 mm in length and about 12 mm wide and carry a small, almost flat shell that measures 11-13 mm in length. Their body color is a translucent beige with flecks or stripes of black pigment. Little is known about the natural history of *Omalonyx*. Hermann & Dundee (1967. *Sterkiana*, 28: 1-6) record observations on *Omalonyx unguis* from Ecuador and mention finding *O. felina* living beneath brush on the moist soil of a steep bank beside a permanent stream.

A small colony of *Omalonyx felina* was maintained in the Museum of Zoology, The University of Michigan over a period of several years. The snails are easily raised in small containers partly filled with moist sand or paper towels. At temperatures above 21° C, the snails grow and reproduce well on a diet of lettuce, chalk and powdered cereal.

This study was undertaken to examine some aspects of the life history of *Omalonyx felina* under "ideal" conditions (i.e., relatively constant temperature and humidity, unlimited space and food, and no disease or predation). Fairly complete records were kept on the growth, mortality and reproduction of 77 individual snails over 2 years. Cohorts of 10 to 25 eggs (laid on the same day) were isolated and studied throughout the slugs' life spans. Clutches of 1 to 2 to 35 (average 13) eggs were found along the walls of the containers. The eggs hatched within about 15 (11-20) days and the small snails were mature within 2 months after hatching. Egg laying occurred in all seasons and throughout the snails' adult lives. Fewer eggs were laid just at maturity and at extreme old age, and the eggs laid at these times were smaller than the usual 2 mm diameter. Mortality was negligible in the egg and hatchling classes but increased drastically when reproduction began. Some snails lived up to 7 months, but most died after 2 months of egg laying. The 77 snails produced 10,855 eggs over a period of 30 weeks.

Detailed data from which the above observations were made were organized into a life table for the population. The products of the values of the survivorship (l_x) and the fecundity (m_x) for each age class (averaged over 2-week periods) were summed, giving a value of 5374 for R_0, the net rate of increase. This shows that the laboratory population is capable of expanding at a tremendous rate. The extremely high net rate of increase obviously is not natural (for a stable population, $R_0 = 1$). The low egg and hatchling mortality is probably the main cause of the discrepancy.

It would be interesting to compare this population with a natural one of *Omalonyx felina* and to compare this species with field and laboratory populations of temperate succineids.

THE STRUCTURE, CILIATION AND FUNCTION OF THE LIPS OF BIVALVES

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Abstract

A study of 12 species of lamellibranch bivalves has provided evidence to support my prediction (Gilmour, 1964, *J. mar. biol. Assoc. U.K.*, 44: 485-498) that the lips of monomyarian anisomyaria would be hypertrophied, but it has also suggested that my ideas on the function of the lips of bivalves are of more general application.

I suggested previously that in a typical dimyarian bivalve with symmetrical anterior and posterior regions the cross-sectional area of the distal oral groove between the labial palps would be much smaller than the cross-sectional area of the anterior regions of the mantle cavity. There would therefore be a reduction in the velocity of the water currents, created by the cilia of the food collecting ctenidia and the food selecting palps, when they emerged from between the palps into the anterior region of the mantle cavity. The water currents would therefore not interfere with the passage of food to the mouth along the proximal oral grooves between the lips. I postulated that it would only be in the monomyarian anisomyaria (in which the water currents would be intensified by the reduction of the anterior regions of the mantle cavity) that these currents would tend to interfere with the passage of particulate material to the mouth.

Examination of the bivalves listed in Table 1 shows that the lips of the monomyarian families Pteriidae, Pectinidae, Limidae and Ostreidae are indeed hypertrophied. But my examination of species of the families Arcidae, Mytilidae and Pinnidae has shown that the lips of non-monomyarian bivalves are not as simple in

TABLE 1. Bivalves examined for lip structure.

Following the classification of Newell (1969)	Species Examined	Following the classification of Thiele (1935)
Class Bivalvia		Class Bivalvia
Subclass Pteriomorphia		
Order Arcoida		Order Taxodonta
Family Arcidae	*Arca noea* Linné	Family Arcidae
Order Mytiloida		Order Anisomyaria
Family Mytilidae	*Modiolus barbatus* (Linné)	Family Mytilidae
Family Pinnidae	*Pinna nobilis* Linné	
Order Pterioida		
Family Pteriidae	*Pteria hirundo* (Linné)	Family Pteriidae
Family Pectinidae	*Pecten maximus* (Linné)	Family Pectinidae
Family Spondylidae	*Spondylus gaederopus* (Linné)	
Family Limidae	*Lima scabra* (Born)	Family Limidae
	Lima hians (Gmelin)	
	Lima subauriculata (Montagu)	
	Lima bronniana (Dall)	
Family Ostreidae	*Ostrea edulis* Linné	Family Ostreidae
Family Anomiidae	*Pododesmus macroschisma* Deshayes	Family Anomiidae

structure and function as Bernard's (1972, *Can. J. Zool.*, 50: 53-57) discussion of the occurrence and function of lip hypertrophy in the Anisomyaria would suggest.

This finding of hypertrophy of the lips in the heteromyarian Mytiloida and the dimyarian Arcoida disproves my previous thesis that the water currents emerging from the lip-apparatus have been intensified by the reduction of the anterior regions of the mantle cavity only in monomyarian bivalves. Even within the monomyarian Limidae, this study of 4 species has shown that the lips can range in complexity from the very simple in *Lima subauriculata* to the very complex in *L. hians*. But this study has also shown that the lips of a wide variety of lamellibranch bivalves can be hypertrophied to prevent the loss of food in water currents produced by their food collecting apparatus and of too great a volume to be swallowed.

It would appear therefore that the development of devices for allowing the escape of excess water driven along with food towards the mouth by the food collecting cilia is of widespread occurrence in suspension feeding bivalves. The possession of such a filtering system is of course universal in suspension feeding members of the echinoderm Superphylum. But whereas in members of the echinoderm Superphylum the development of gill slits to allow the escape of excess water which has already entered the mouth has had great evolutionary implications, the escape of water before it gets to the mouth is usually achieved in a less conspicuous manner in bivalves, although a complex lip-apparatus has been developed in some monomyarian members of the Pteriomorphia.

THE STRUCTURE OF CALCAREOUS SNAIL EGGS

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Abstract

While the structure and biology of the basommatophoran egg has received some attention, the study of the stylommatophoran egg has been much neglected. Currently, a major research effort is being devoted to the investigation of the biology of the calcareous snail egg.

The term "calcareous egg" can be defined as any egg which has $CaCO_3$ in crystalline, insoluble particles, or aggregates of such particles, around or within the egg jelly. One may divide calcareous eggs into 2 kinds:

1) partly calcified eggs - with discrete, individual particles of $CaCO_3$, where the particles do not form a solid shell, e.g., *Triodopsis multilineata, Helix pomatia.*
2) heavily calcified eggs - with a hard, brittle shell of $CaCO_3$, somewhat like a hen's egg, e.g., *Anguispira alternata, Cepaea nemoralis.*

Thus far, in the survey of the order Stylommatophora, calcareous eggs have been found in the Orthurethra, Mesurethra and Sigmurethra. Within the Sigmurethra, they are found in all 3 infraorders, Holopopoda, Aulacopoda and Holopoda.

Analysis of the composition of the crystals in the calcareous eggs reveals that it is $CaCO_3$ in the form of calcite. The body shell of the snail - as contrasted with the egg shell - is in the form of aragonite.

The biological significance of this observation is not known. However, if one compares the physical differences between calcite and aragonite, at least one explanation presents itself. Aragonite is more dense, stronger, and is less prone to breaking or cleaving than calcite. Thus, given the choice between a calcitic and an aragonitic body shell, the aragonitic shell can better withstand the abrasion by particles of soil and rock. Calcite, on the other hand, is more economical to secrete because it occupies more space per mole of $CaCO_3$ secreted. Thus, the snail eggs, not subjected to mechanical wear and abrasion, are of calcite rather than aragonite.

BEHAVIORAL AND PHYSIOLOGICAL STUDIES ON LOCOMOTION IN THE GIANT GARDEN SLUG, *LIMAX MAXIMUS*[1]

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Abstract

The patterned muscular activity of the gastropod foot is involved in an array of behavioral acts. Food seeking and homing clearly involve normal locomotion, while the righting responses of some gastropods (i.e., *Limax* and *Haliotis*) involve "locomotor-like" actions of the foot. With locomotion being involved in an array of behavioral acts, it is requisite for our understanding of gastropod behavior to have a clear picture of the neural organization underlying control of locomotion.

The well-developed pedal musculature and synchronous pedal waves of the slug, *Limax maximus*, make this species an excellent choice for a study of gastropod locomotion.

The foot of *Limax maximus* is differentiated into 3 longitudinal bands of musculature. The median band produces pedal waves and the 2 lateral bands make smooth secure contact with the substrate. Viewing the ventral surface of a *Limax* foot (while the slug moves on a sheet of glass) reveals that at the onset of movement, the initial pedal waves appear at the anterior-most part of the foot surface. As the animal moves forward, pedal waves move anteriorly along the pedal band. We have measured several parameters of the pedal waves on 15 small slugs (weight range: 1.0 - 0.56 gm). The measurements were made as the slugs crawled up the inner wall of a graduated cylinder. Our findings are summarized as follows:

Pedal wave length	Animal walking length
mean: 0.34 cm (range: 0.24 - 0.48 cm)	mean: 4.6 cm (range: 3.8 - 4.8 cm)
Pedal wave velocity	Animal walking velocity
mean: 29.9 cm/min.	mean: 13.2 cm/min.
range: 21.4 - 36.8 cm/min.	range: 8.14 - 20.6 cm/min.

Although we observed a lower wave velocity/animal velocity ratio than that reported by Crozier & Pilz (1923, *J. gen. Physiol.*, 6: 711-721), the ratio does seem to reflect a fixed relationship.

The removal of the central nervous system (CNS) from a mollusc usually does not abolish all reflex muscle activity. For example, tactile stimulation of clam siphons isolated from the CNS results in a reflex withdrawal response (Prior, 1972, *J. exp. Biol.*, 57: 133-145). These local reflexes are mediated by peripherally located neural elements. When studying molluscan behavior, one must consider the relative roles of the central and the peripheral neural elements.

Some uncertainty has remained with regard to the control of the pedal waves produced by *Limax*. Kunkle (1903, *Zool. Anz.*, 26: 560) reported that when the foot of *Limax* was cut into small pieces, pedal waves persisted on each piece. Largely on the basis of this report, it has been concluded that in the case of *Limax*, the CNS is not necessary for normal pedal wave activity (Bullock & Horridge, 1965, *Structure and function in the nervous systems of invertebrates*. W.H. Freeman, San Francisco).

We have repeated, and modified in some cases, the experiments of Kunkle. When blood pressure was maintained in the posterior portion of a decapitated slug (by tying a string around the body at the level of the mantle attachment), sequential pedal waves were observed for at least an hour. The pedal waves were weak and ill-formed, but did proceed in normal fashion along the pedal band. From this it can be concluded that peripheral neural elements are sufficient for the production of sequential pedal waves. As expected,

we found neuron cell bodies at the branching points of the posterior pedal nerves of *Limax*. These neurons, which are part of the peripheral system, may be involved in production of the patterned pedal wave activity.

One would like to compare the results obtained from decapitated animals with observations of healthy animals with partially denervated feet. We have surgically severed both main posterior pedal nerves (PPN) in slugs anesthetized with CO_2. Following recovery from the anesthesia (about 20 min.), the posterior 1/3 of the foot was contracted and lacked pedal waves, while the anterior portion produced normal pedal waves. These slugs have been kept for up to 3 months following surgery and at no time have the denervated portions of the feet shown any sign of pedal waves. Following section of only 1 of the 2 PPNs, we observed no alterations in the pedal wave activity.

These results indicate that activity from the CNS is necessary, at least, to initiate pedal wave activity. The view that the CNS initiates and modulates pedal waves is supported by the observations that (in healthy animals) the velocity of pedal waves is variable and that occasionally waves appear on only a portion of the pedal band (i.e., when making a hair-pin turn). Neither changes of velocity nor partial cessation of wave activity are seen in decapitated preparations.

We tentatively conclude that neural control underlying pedal wave activity is a function of a peripheral network capable of generating the rudimentary pedal wave pattern but which requires central nervous system initiation and modulation for normal operation.

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[1]Supported by National Science Foundation Grant GB 20762 to A. Gelperin. D.J. Prior was a Spencer Foundation Fellow in Neurobiology.

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COMPARATIVE ASPECTS OF THE MORPHOLOGY AND PHYSIOLOGY OF A SINGLE IDENTIFIABLE NEURON IN *HELIX ASPERSA*, *LIMAX MAXIMUS* AND *ARIOLIMAX CALIFORNICA*[1]

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Abstract

There is a single, conspicuous giant neuron in each metacerebral ganglion of the following Stylommatophora: *Helix aspersa*, *H. pomatia*, *Limax maximus*, *L. flavus*, *Derocerus reticulatus*, *Milax budapestensis*, *Arion ater*, *A. hortensis*, *Ariolimax californica* and *Achatina fulica*. A considerable amount of information is available on the electrophysiological, biochemical and morphological properties of this cerebral giant cell (CGC) in the snail, *Helix aspersa* (e.g., see Osborne & Cottrell, 1972, *J. Neurochem.*, 19: 2363-2368). However, little attention has been directed toward the elucidation of these neuronal properties of the CGC in other species. We believe the wide distribution of the CGC offers an unique opportunity for the comparative study of a single, identifiable neuron in a large number of readily available gastropod mollusks. Further, we believe such information is necessary for a deeper insight into the cellular mechanisms underlying the evolution of animal behavior.

Our initial efforts have been concentrated on *Helix aspersa*, *Limax maximus* and *Ariolimax californica*, which represent both the Holopoda and Aulocopoda divisions of the order Stylommatophora. For this study, conventional electrophysiological recording techniques were employed. Intracellular dye injection of procion yellow or cobalt chloride was also used to determine the 3-dimensional morphology of the cells under investigation.

Similarities. In every individual of all species studied to date, the CGC had processes that emerged from ipsalateral cerebral ganglion only in the cerebral-buccal connective or the external lip nerve. In *Ariolimax californica*, the processes in the cerebral-buccal connective made excitatory monosynaptic connections with the 2 largest neurons in the buccal ganglion near the entry of the connective. A similar finding has been reported for *Helix aspersa* by Cottrell (1971, *Experientia*, 27: 813-815). In *Helix*, *Limax* and *Ariolimax*, a more medially located, large buccal neuron is excited by the CGC, most probably through a polysynaptic pathway.

In addition to these electrophysiological and morphological similarities, work in other laboratories (e.g., see Osborne & Cottrell, 1971, *Z. Zellforsch.*, 112: 15-30) have shown the CGCs of several species, including *Helix* and *Limax*, to contain considerable concentrations of 5-hydroxytryptamine, the presumptive neurotransmitter for this neuron.

Differences. In addition to the ipsalateral processes, the CGC in both *Helix* and *Ariolimax* have a prominent process in the cerebral commissure that transverses the contralateral metacerebrum and exits via the contralateral cerebral-buccal connective. In no instance could a similar process be demonstrated for the CGC in *Limax* either by dye injection or by electrophysiological techniques. Dye injection of another limacid slug, *Derocerus reticulatus*, also failed to show any process in the cerebral commissure though processes in the ipsalateral cerebral-buccal connective and external lip nerve filled well.

In *Helix*, the functional significance of this commissural process remains obscure, while in *Ariolimax*,

this process makes an electrical synapse with the contralateral CGC before exiting via the contralateral cerebral-buccal connective. The reciprocal electrical coupling thus produced is sufficiently strong to produce synchronous firing of both CGCs under certain conditions.

Conclusions. Though we have discovered some significant differences, the great similarity in morphology, biochemistry and connectivity of the CGCs in the 3 species investigated can best be explained by assuming a common phylogenetic origin. This leads us to propose that the CGCs found in the Stylommatophora represent homologous neurons. If further investigation shows differences in neuronal properties to be correlated with known phylogenetic relationships, the case for homology will be strengthened. Rigorous proof, however, must await the development of suitable embryological and genetic analyses. Nevertheless, it is our belief that the differences mentioned above most likely represent cellular changes underlying behavioral evolution.

[Note added in proof. Investigations in other laboratories have now identified a pair of giant serotonergic neurons in the cerebral ganglia of the following opisthobranchs: *Aplysia californica*, *Tritonia diomedia* and *Pleurobranchaea californica*. The clear similarities between the CGCs in both the pulmonates and the opisthobranchs extends the phylogenetic limits in which CGC homologues can now be recognized.]

[1]Supported (in part) by a research grant (NSF-GB-20762) from the National Science Foundation to Dr. A. Gelperin and a pre-doctoral fellowship from the Spencer Foundation to D. Senseman.

* * * *

THE HISTOCHEMICAL IDENTIFICATION OF GALACTOGEN IN THE SUCCINEIDAE[1]

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Abstract

Galactogen is a galactose polymer shown to be present in the albumen gland of every pulmonate studied thus far. In addition, galactogen is present in the eggs of pulmonates. The Succineidae have been little studied in regard to galactogen, with the exception of George & Jura (1958, *Proc. K. ned. Akad. Wetensch.*, 61: 598-603), whose work hinted at the presence of galactogen in the eggs of *Succinea putris*. In the present work, 3 species of succineids, representing 3 genera, were studied: *Catinella vermeta*, *Omalonyx felina* and *Oxyloma retusa*. Paraffin sections were made of albumen glands fixed in either Bouin's fixative or in 2% calcium acetate in 10% formalin. Galactogen was determined by the staining reactions recommended by Grainger & Shillitoe (1952, *Stain Technol.*, 27: 81-85). All 3 species showed identical staining reactions, and the presence of galactogen was confirmed in the albumen glands of these species.

[1]Supported, in part, by PHS Training Grant No. 5 T1 AI 41 from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

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ORGAN CULTURE OF *HELIX POMATIA* ALBUMEN GLAND IN A DEFINED MEDIUM

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and

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Abstract

Land and freshwater gastropods of temperate climates have a seasonal rhythm of summer egg laying and winter hibernation. Still unknown are the biochemical factors which may control the cycles of reproduction and hibernation in these animals.

It may now be possible to identify these factors through organ culture of the albumen gland. This gland exhibits a seasonal pattern of polysaccharide synthesis (May, 1934, *Z. Biol.*, 95: 401-430). In autumn, glycogen is synthesized and stored in the gland as well as in other tissues. This food reserve is slowly catabolized during winter hibernation. In spring the galactogen is synthesized (Goudsmit & Ashwell, 1965, *Biochem. Biophys. Res. Comm.*, 19: 417-422) and accumulates specifically in the albumen gland. This galactose homopolymer is presumably a food reserve for the developing embryo, as it is the sole carbohydrate component of the embryonic perivitelline fluid and is catabolized during development. Thus, activation and/or inhibition of galactogen and glycogen metabolism could provide an assay for the presence of the biochemical factor(s) responsible for triggering egg-laying (increased galactogen synthesis) and hibernation (increased glycogen synthesis).

We wished to approach this problem by utilizing organ culture. Such a system is as close to the *in vivo* situation as possible while still being amenable to quantitation, specific biochemical experimentation and analysis.

We now report: 1) the successful maintenance of the *Helix pomatia* albumen gland in organ culture in a chemically defined medium and 2) a method for the determination of the specific activity of galactogen-C^{14} and glycogen-C^{14} in the same preparation.

One freshly excised albumen gland was weighed, washed in 3 changes of physiological saline (Ripplinger & Joly, 1961, *Soc. Biol.* (Lyon), 155: 825-827) containing penicillin, cut into 2 mm cubes and transferred to the culture medium. The explants in sterile petri dishes rested upon a semi-solid base of agar:peptone: Geys solution (1:1:98). The nutritive medium (9.0 ml) contained by volume: M-199 (5.0%), Tyrodes solution (45.0%), $NaHCO_3$ (2.5%), yeast extract (0.1%), penicillin (300 units/ml), and .01M Hepes buffer pH 7.5 (47.0%). The osmolarity was adjusted to correspond to that of the snail's hemolymph. This was 160 milliosmoles or 140 milliosmoles for hibernating or active snails respectively.

The explants remained alive for at least 2 weeks without changing the nutritive medium. Viability of the albumen gland in culture was determined by the clearly visible ciliary beat of centrotubular cells.

In order to ascertain the degree of galactogen and glycogen synthesis by an albumen gland in organ culture, .75 μcurie of glucose-C^{14} (s.a. 6.9 mc/mm, ICN-California) was added to the nutritive medium. The explants from one gland were harvested after 30 minutes, 4 days and 8 days in organ culture and the specific activity of glycogen-C^{14} and galactogen-C^{14} measured. The polysaccharides were extracted from 5N KOH digests of pooled explants by repeated precipitation with ethanol. The polysaccharides were redissolved in distilled water, further purified by dialysis against distilled water. Galactogen and glycogen were then separated. Glycogen was removed from solution by co-precipitation with concanavalin A (Calbiochem). Galactogen remained in the supernatant solution. The precipitant and supernatant fractions were each hydrolyzed in 2N H_2SO_4, neutralized with $BaCO_3$. The hydrolysate from the supernatant fraction when chromatographed (butanol:pyridine:water, 10:4:3) contained galactose-C^{14} as the sole radioactive component. The amount of galactose recovered was determined by the galactostat assay (Worthington). The precipitant fraction contained glucose-C^{14} as the only product.

Our results show that the albumen gland in organ culture incorporates C^{-14} into both galactogen and glycogen and the uptake of isotope is linear with time for at least 8 days.

We are now using the method developed to investigate the effect of snail extracts in the culture medium on the rate of galactogen-C^{14} and glycogen-C^{14} synthesis by the albumen gland.

A detailed account of this work is being prepared for publication.

A SIMPLE BIOCHEMICAL METHOD FOR DISCERNING BETWEEN DIPLOID AND POLYPLOID SPECIES OF THE *BULINUS* (*ISIDORA*) COMPLEX[1]

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Abstract

After many years of making electrophoretic separations of *Bulinus* (*Isidora*) populations from Africa and staining these gels for non-specific esterases, it became evident that there was a wide variation in the total esterase activity between the 2 major chromosomal groups. Isozymes of the diploid (n=18; 2n=36) populations have a greater esterase activity and more dense bands than do the tetraploid (n=36; 2n=72) populations, when the esterases are separated and stained on polyacrylamide gels. With this in mind, it was our hope to develop a fast and simple test tube procedure to distinguish between these 2 groups without resorting to electrophoresis, immunology, chromosome studies or other complicated methods. Preferably, such a test would be one that could be performed in the field.

We have now developed a relatively simple procedure to distinguish diploid and tetraploid bulinine species of the *Isidora* group. The stock solutions used are the same as those used in the electrophoresis staining (Hunter & Markert, 1959, *J. Histochem. Cytochem.*, 10(6): 677; (7): 42-49), i.e., pH 7.4 tris-HCl buffer; 1% α-napthylacetate in acetone; Blue RR solution 35 mg/ml; ethyl acetate. The procedure is as follows. A sample of snail foot tissue (3.5 - 6.5 mg) containing esterases and other proteins is homogenized in 0.2 ml of 7.4 tris-HCl buffer and centrifuged. The resulting supernatant fluid is transferred to a larger 20 ml test tube, to which is added 2 ml of esterase stain containing 41 ml of distilled water, 8 ml buffer, 1 ml α-napthylacetate and 1 ml Blue RR solution. The mixture is placed in the dark at room temperature for 15 minutes. The test tubes are removed from the dark, and 5 ml of ethyl acetate is added to each tube and shaken; this extracts the color from the aqueous phase of the mixture. The test tube is then allowed to stand (with occasional shaking) for 15 minutes so that the extraction will be complete. The upper fraction is placed in a suitable colorimeter tube and the results observed in a colorimeter at 405 mμ. The absorbance of light is divided by the wet weight of tissue to obtain a decimal fraction. If this number is greater than 0.100, the snail is a normal haploid (n=18) species. If the number is less than 0.100, the snail is a tetraploid (n=36) species. However, the difference in color density between the 2 chromosomal groups is quite pronounced, and we have had no trouble in distinguishing between them with the unaided eye. Therefore, a colorimeter is not always necessary. (A color comparison can be made with a standard known snail or from a photograph of previous reactions.)

Given an incubation time of 15 minutes, approximately 5.0 mg of tissue gives the best color density for use in a colorimeter. This weight is less than that of a foot from any adult *Bulinus* (*Isidora*) specimen, so individual snails can be tested. In our laboratory, we find it convenient to weigh 5 mg of tissue and homogenize this weight with a sonic probe in 0.2 ml of buffer, but several variations can be made which will give the same results and allow the use of less expensive and less bulky equipment.

Because of the extraction step the volume of supernatant is not important, so the tissue can be homogenized in as much as 1 ml of buffer using a hand homogenizer. Or, 50 mg of the pooled tissue can be weighed using a less sensitive balance, homogenized with a hand homogenizer and 0.2 ml of the resultant supernatant used for the test. By making some simple adjustments in the procedure, this test can be used in most laboratories, as well as in the field.

[1]Supported, in part, by grants from the Office of International Activities, Smithsonian Institution and the Rockefeller Foundation (GA BMS 7215).

THE GENUS *BULINUS* AND SCHISTOSOMIASIS IN NORTH AFRICA[1]

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Abstract

Schistosomiasis haematobia occurs in North Africa in Morocco, Algeria and Tunisia. In Morocco, the endemic foci are divided into 3 major regions: 1) in the north, including the towns of Souk-el-Arba-du-Rhab, Ksar-el-Kebir and Larache; 2) in the southwest in the Souss Valley; and 3) in the southeast in the region of Ksar-el-Souk, and extending to Tafilalet.

In Algeria, there are 4 known areas of urinary schistosomiasis. Two are in the north: Foundouk at the Barrage du Hamiz and St. Aimé de la Djidioua; and 2 are in the south: Djanet and El Ouata. The 2 foci in the south have been undergoing a regression during the last 10 years.

In the south of Tunisia, the endemic foci of schistosomiasis haematobia occur in the oasis areas of Gabes, El Hamma, Kebili, Douze, El Faouar, Gafsa, Tozeur and Nefta. Currently, there is an effective anti-bilharzia program in most of these areas.

The snail intermediate host in North Africa is reported to be *Bulinus truncatus* (e.g., see Mandahl-Barth, 1957, *Bull. Wld. Hlth. Org.*, 17: 1-65; Mandahl-Barth, 1960, *Bull. Wld. Hlth. Org.*, 22: 565), although none of the populations have been studied in regard to the most reliable criteria for snail identification, i.e., chromosome numbers (see Burch, 1960, *Z. Tropenmed. Parasitol.*, 11: 449-452; Burch, 1964, *Malacologia*, 1: 387-400); immuno-taxonomy (Burch & Lindsay, 1970, *Malacol. Rev.*, 3: 1-18); and electrophoresis (Burch & Lindsay, 1967, *Amer. malacol. Union, ann. Reps.*, 34: 39-40; Wright & Ross, 1965, *Bull. Wld. Hlth. Org.*, 32: 709-712; Malek & File, 1971, *Bull. Wld. Hlth. Org.*, 45: 819-825).

In early 1973, we initiated a program to study *Bulinus* in North Africa, and during the months of June and July 1973, we collected specimens from Ksar-el-Kebir and Rhedira, Morocco; Barrage du Hamiz, Algeria; and El Faouar, Tunisia. Many other areas were visited, but no bulinine snails were found.

Laboratory studies currently underway using cytological and biochemical techniques on these snails should determine their relationships to the more thoroughly studied bulinine species in other parts of Africa.

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[1]Supported by research grants from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service (N. I. H. Training Grant No. 5 T1 AI 60), the Smithsonian Institution (SF3-00110) and the Rockefeller Foundation (GA BMS 7215).

BIOLOGY AND CONTROL OF *BULINUS TRUNCATUS* IN EGYPT[1]

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Abstract

A semi-field study has been recently made of seasonal growth, mortality, productivity and changes in population density of the snail *Bulinus truncatus*, the transmitter of urinary schistosomiasis in Egypt. Observations were made on 3 populations of different sizes and ages, maintained in 3 earth-lined artificial ditches with continuously flowing Nile water. Standard semi-monthly samplings with a dip-net were regularly made of each population over a period of 1 year. The sampled snails were measured and the size-frequency distributions of successive samples were used to study average growth, mortality and productivity during successive half-month periods between samplings.

The data reveled that the annual cycle of this species in Egypt is mainly dependent upon seasonal changes in environmental temperatures. Considerable breeding and little mortality occur in winter. The relatively few snails which survive the annual "winter closure" of water in the irrigation network (extending throughout January) start breeding as soon as the closure is over. A "winter" generation of young snails makes its appearance and the snail populations start building up gradually as a consequence. As the environmental conditions further improve in spring, a second or "spring" generation is produced and the snail populations expand more rapidly, until a major density peak is reached in or around June. Egg production then diminishes and mortality greatly increases as the water temperatures continue to rise in summer. This results in quick and sharp population declines in late summer. The few survivors start breeding some time in autumn. A third or "autumn" generation is therefore produced and the snail populations build up again, until a minor density peak is attained in November or December.

At the present time, a country-wide snail control program adopted by public health authorities in Egypt concentrates on attacking schistosome snail vectors with molluscicides in late spring, when they are most numerous and schistosome infection rates among them are highest. This attack causes only temporary reductions in the snail populations during the main transmission period of the disease, but it has hardly, if ever, prevented the snail populations from recovering their initial high densities every spring.

A new schedule for snail control work in Egypt is proposed which is hoped to bring about better results. Mass molluscicide, as is now being performed in May-June, is recommended in October-November, followed by general snail surveillance and individual treatments of reinfested streams in April-June. The suggested autumn mass treatment would reinforce the deleterious effects on snail populations of excessive heat in late summer, and would itself be followed by drought during the "winter closure" of water in January. It should cause a greater damage to the snail populations, thereby minimising the chances for reinfestation and snail population recovery in the following spring.

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[1]The full paper is published in "Proceedings of the Egyptian Academy of Sciences," 1972, 25: 37-60.

EXPERIMENTAL INFECTION OF *BULINUS SERICINUS* WITH *SCHISTOSOMA HAEMATOBIUM*[1]

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Abstract

Bulinus sericinus (Jickeli 1874) was the first bulinine snail to be named from the Ethiopian highlands. We have previously shown (Wu & Burch, 1973, *Malacol. Rev.*, 6(1): 62-63) the close morphological, cytological and biochemical relationship of *Bulinus sericinus* to *Bulinus truncatus*, the latter being the intermediate host of the human blood fluke *Schistosoma haematobium* in the Near East and Africa north of the Sahara. Both snail species are tetraploid (n=36, 2n=72), each species having twice the chromosome number characteristic for the family Planorbidae (x=18). A close relative, *Bulinus tropicus*, which is common to much of Africa south of the Sahara, is nearly always non-susceptible to human schistosome infection. In Ethiopia not only do the diploid *Bulinus tropicus* and the tetraploid *Bulinus sericinus* occur, but also a hexaploid (n=54, 2n=108), *Bulinus hexaploidus*, and an octoploid (n=72, 2n=144), *Bulinus octoploidus*.

The susceptibility of the Ethiopian polyploids to *Schistosoma haematobium* has not been studied, except for Lo's (1972) report of 7% infection of *Bulinus octoploidus* with an Egyptian strain of the parasite. Wright (1963, *Trans. Roy. Soc. trop. Med. Hyg.*, 57: 142-147) failed to infect so-called *"Bulinus sericinus"* of western Aden with the local strain of *Schistosoma haematobium*, although Lo (1972, *Malacologia*, 11(2): 225-280) did get 24% infection of presumably the same western Aden species with the Egyptian strain of the parasite. Our present study reports the infectivity results of exposing Ethiopian *Bulinus sericinus* from its type locality, the Toquor River at Mekerka, to 4 strains of *Schistosoma haematobium* (from Egypt, Iran, Liberia and Rhodesia). *Bulinus sericinus* was refractory to the Rhodesian strain of parasite, although it was infected with the other 3 strains: 52.6% with the Egyptian strain, an average of 14.8% with the Iranian strain, and an average of 2.15% with the Liberian strain.

Human schistosomiasis haematobia occurs in Ethiopia, principally in the lower eastern regions of the country (for example, the Awash River valley, where the snail species transmitting the disease is *Bulinus* (*Physopsis*) *abyssinicus*). In the Ethiopian northern highlands, cases of schistosomiasis haematobia reported previously were evidently imported and unknown in origin (see Ayad, 1956, *Bull. Wld. Hlth. Org.*, 14: 1-117).

At present, we do not have an Ethiopian strain of *Schistosoma haematobium* with which to test susceptibility of *Bulinus sericinus*. Since the intermediate host of *S. haematobium* in the eastern lowlands of Ethiopia is a member of the bulinine subgenus *Physopsis*, species of which at present are not known to occur in the Ethiopian highlands, one might suspect that this particular Ethiopian strain of schistosome would not infect the highland *B. sericinus*. And, in our studies, *B. sericinus* was not susceptible to the Rhodesian strain of *S. haematobium*, which also uses a *Physopsis* species as its intermediate host. However, *B. sericinus* did show a low rate of infection to the Liberian schistosome strain, a strain which goes through a *Physopsis* species. This then would indicate that *B. sericinus* may possibly be a potential transmitter of eastern Ethiopian schistosomiasis haematobia. But, perhaps more important is the fact that *B. sericinus* is highly susceptible to the Egyptian strain of *S. haematobium* and moderately susceptible to the Iranian strain, thereby indicating that if the northern African and Near Eastern human schistosomes came into the country, a satisfactory snail host is on hand to maintain them.

[1]Supported, in part, by grants from the Office of International Activities, Smithsonian Institution and the Rockefeller Foundation (GA BMS 7215). We wish to thank E.G. Berry and I. Dombo for the supply of schistosome strains used in this study.

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THE LARVAL INTERACTION OF *PARAGONIMUS OHIRAI* AND *SCHISTOSOMA JAPONICUM* IN *ONCOMELANIA*[1]

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Abstract

It has been suggested previously (LoVerde & Yasuroka, 1972, *Malacol. Rev.*, 5: 14) that the genus *Oncomelania* may serve as a model to study the larval interaction of *Schistosoma japonicum* and the rat lung forms of *Paragonimus*. To date, the models of larval interaction have been limited to pulmonate snails, with echinostomes and *Schistosoma mansoni* receiving the most attention (see Lim & Heynemann, 1972, *Adv. Parasitol.*, 10: 191-268 for a review). The present study is on *P. ohirai* and *S. japonicum*.

Three hundred and fifty specimens of *Oncomelania hupensis* ssp. were divided into 7 lots of 50 each. Each snail was exposed individually to 5-8 miracidia of either *Paragonimus ohirai* or *Schistosoma japonicum* (or both) at a constant temperature (24°C) and maintained 10 to a Petri dish under constant and identical conditions. Snails challenged with the second parasite were also exposed to 5-8 miracidia each and maintained under the same identical conditions.

One hundred and fifty snails divided into 3 lots of 50 snails each were exposed to *Schistosoma japonicum* and then challenged with miracidia of *Paragonimus ohirai* at 30, 60 and 90 days, respectively. One lot of 50 *Oncomelania* was exposed to both *S. japonicum* and *P. ohirai* within a 24 hour period. The remaining 150 snails were divided into 3 lots of 50 each and were exposed to *P. ohirai* and then challenged with miracidia of *S. japonicum* at 30, 60 and 90 days, respectively. Controls were employed in all cases. Snails were removed at regular intervals, some for direct observation, others for dissection, and still others for histological examination. Results of the histological examination will be reported at a later date.

In the 3 lots of *Oncomelania* exposed to *Schistosoma japonicum* and later challenged with *Paragonimus ohirai*, the larval parasites of both species were able to co-exist in the same snail. *P. ohirai* miracidia were able to penetrate the *S. japonicum* infected snails, develop into rediae and eventually produce cercariae, even in those schistosome infected snails that were patent.

When *Oncomelania* were exposed to miracidia of both *Schistosoma japonicum* and *Paragonimus ohirai* within the same 24 hour time period, all of the 30 snails examined had *P. ohirai* infections. In 3 cases (10%) both parasites were able to develop in the same snail and both eventually produced cercariae. When the snails were exposed first to *P. ohirai* and then later challenged with *S. japonicum*, 7 (8%) of the 91 paragonimus-positive snails observed also had schistosome infections. Control snails (exposed only to *S. japonicum*) had a 46% incidence of infection. On the other hand, when schistosome snails were later challenged with *Paragonimus*, 83 (90.2%) of the 92 snails observed had double infections. Control snails (exposed only to *P. ohirai*) had a 98.6% incidence of infection.

The data indicates that larval antagonism occurs between the 2 parasites, i.e., *Paragonimus ohirai* is antagonistic to *Schistosoma japonicum*, and the antagonism is most evident when *P. ohirai* has been established in the snail prior to schistosome challenge. Antagonism is also evident, but to a smaller degree, if the snails are exposed to both parasites at about the same time. Direct antagonism was not observed, but evidence from dissections of the snails indicated that the nature of the antagonism was indirect. Whether or not *S. japonicum* exerts a counter antagonistic effect on *P. ohirai* was not clearly evident from the data.

[1]This investigation was supported, in part, by PHS Training Grant No. 5 T1 AI 60 from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service, and, in part, by a grant (DA-49-193-MD 2651) from the U.S. Army Research and Development Command. We wish to acknowledge the aid of Dr. Yukio Hosaka, National Institute of Health, Tokyo, Japan, in obtaining the ova of *Paragonimus ohirai*.

Biologists attending the Mollusk Seminar, Ann Arbor, Michigan, U.S.A., 24-25 August 1972. Left to right: J. B. Burch, David Senseman, Paul H. Rudolph, David J. Prior, Emile S. Demian, Amy L. Shrader, Carol B. Stein, George A. Te, David H. Stansbery, Philip T. LoVerde, C.M. Patterson, T. H. J. Gilmour, Virginia A. Vail, William H. Heard, James N. Cather, Alex S. Tompa, Esther M. Goudsmit, Lyford K. Greene, William A. Sodeman, Mark J. Camp, Y. S. Liang.

ANNOUNCEMENTS AND NEWS

MEETING OF THE INSTITUTE OF MALACOLOGY. — A meeting of the Institute of Malacology was held at the Academy of Natural Sciences, Philadelphia, on December 7, 1973, presided over by the President, Dr. Norman F. Sohl. In addition to the president, the meeting was attended by Kenneth J. Boss, J. B. Burch, George M. Davis and Robert Robertson. The main business discussed was the affairs of *Malacologia*, the International Journal of Malacology, and the transfer of its editorial offices to the Academy of Natural Sciences. Elected to Sponsor Membership in the Institute of Malacology were C. J. Bayne, Clyde F. E. Roper and S.-K. Wu. The following new officers were elected: President, Robert Robertson; President-Elect, J. B. Burch; Executive Secretary-Treasurer, George M. Davis.

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND, PROGRAM OF MEETINGS FOR 1974. — The meetings of the Conchological Society are held in The Conversazione Room, British Museum (Natural History), Cromwell Road, South Kensington, S.W. 7, England, U.K. at 2:30 p.m. The program of subjects for exhibition and discussion is as follows:

"Spanish Mollusca" — Exhibition, January 19, 1974.
"A Hispanic view of the shell," by Miss E. F. Fogan, January 19, 1974.
Open exhibition — Annual General Meeting, February 23, 1974.
"The history of the Society," by T. E. Crowley, Presidential Address, February 23, 1974.
"Marine and non-marine molluscs of Madeira and the Canary Islands" — Exhibition, March 16, 1974.
"Madeiran molluscs," by C. W. Pettitt, March 16, 1974.
Open exhibition — Conversazione on any molluscan subject, April 20, 1974.
"Conchological books" — Exhibition, May 18, 1974.
"Conchological books," by A. P. H. Oliver and T. Pain, May 18, 1974.
"American marine molluscs" — Exhibition, October 19, 1974.
"West American marine molluscs - some micro-habitats," by M. J. Bishop, October 19, 1974.
"British land Mollusca" — Exhibition, November 16, 1974.
"Natural selection in *Cepaea*," by A. J. Cain, November 16, 1974.
"Freshwater Mollusca" — Exhibition, December 14, 1974.
"Research on ponds," by J. F. Peake, December 14, 1974.

Advance information:

"Pearls, oysters and mussels" — Exhibition, January 18, 1975.
"The cultured pearl," by E. E. Sandor, January 18, 1975.

The Honorable Secretary of the Society is Mrs. E. B. Rands, 51 Wychwood Avenue, Luton, Beds. LU2 7HT, England, U.K.

DEUTSCHEN MALAKOZOOLOGISCHEN GESELLSCHAFT. — Einladung zum Frühjahrstreffen 1974 der Deutschen Malakozoologischen Gesellschaft in Staffelstein vom 23. bis 26. Mai. Staffelstein liegt am Fusse des 539 m hohen Staffelbergs im Durchbruchstal des Obermains durch die Ausläufer des Fränkischen Jura, rund 26 km NNE von Bamberg, 18 km S von Coburg. Zu erreichen ist die 800jährige Adam Riese-Stadt von Bamberg und Coburg aus über die Bahnlinien 810, 820 und 830 sowie auf guten Autostrassen, z.B. von S: Autobahn München-Nürnberg-Berlin (E 6) bis Bayreuth, dann über die "Strasse der Residenzen": B 85 bis Kulmbach - B 289 über Burgkunstadt bis Redwitz - B 173 über Lichtenfels bis Staffelstein; oder: von Bamberg über Hallstadt auf der "Strasse der Residenzen" bis Breitengüssbach, dann auf der B 173 den Main entlang bis Staffelstein; von SW: über die E 70 Stuttgart-Würzburg und auf Autobahn oder Bundesstrassen bis Bamberg und weiter nach Staffelstein wie oben; von NW: über die E 5 Frankfurt-Würzburg-(Nürnberg) bis Ausfahrt Bamberg und über die B 505 nach Bamberg und Staffelstein; von N: über die E 70 Hannover-Kassel-Fulda bis Schweinfurt-N, B 303 bis Schweinfurt und B 26 über Hassfurt nach Bambert, dann wie oben; oder: von Fulda über die B 279 über Gersfeld-Bad Neustadt-Königshofen-Ebern (-Bamberg) nach Staffelstein.

Der individuellen Variation sind keine Schranken gesetzt, um so weniger, als die "Lande um den Main" mit einer Vielzahl herrlicher Schlösser, Klöster, Kirchen und romantischer Fachwerk-Städtchen aufwarten, die eines Abstechers wert sind.

Vorläufiges Programm. Donnerstag, 23. Mai (Himmelfahrt): Eintreffen der Teilnehmer; abends Begrüssung durch den Bürgermeister von Staffelstein und zwangloses Beisammensein. Freitag, 24. Mai: Vormittag: Exkursion Staffelberg (*Helicigona cingulata*) und Umgebung unter Führung von Dr. Hasslein. Nachmittag: weitere Exkursionen. Samstag, 25. Mai: Tagesexkursion mit Bus nach Kloster Vierzehnheiligen, Schloss Banz und Coburg. Unterwegs Gelegenheit zum Sammeln (*Azeca menkeana* bei Vierzehnheiligen, z.Z. verschollen; *Candidula unifasciata rugosiuscula* an der Veste Coburg). In Coburg Besuch des Museums und

gemeinsames Mittagessen. Abends gemütliches Beisammensein im Gasthof zur Post in Staffelstein. Sonntag, 26. Mai: Vormittag: Bamberg - Stadtbesichtigung und gemeinsames Essen. Nachmittag: Rückreise.

Sonstige Anfragen an: Dr. Werner Bolling, D-86 Bamberg, Luitpoldstrasse 33, oder Dr. Günter Schmid, D-714 Ludwigsburg, Favoriteschloss.

WESTERN SOCIETY OF MALACOLOGISTS. — The Seventh Annual Meeting of the Western Society of Malacologists will be held June 19-22, 1974, at the Kellogg West Conference Center on the campus of California State Polytechnic College, Pomona, California, U.S.A. The program will feature contributed papers, symposia, displays and study workshops on molluscan subjects. In addition to the program of research papers, there will be a concurrently running program of popular presentations on shells or shell collecting. Inquiries about the meeting should be made no later than May 15th and should be directed to the Secretary, Mrs. Edith Abbott, 1264 West Cienega Avenue, San Dimas, California 91773. Applications for membership should be sent to the Treasurer, Mr. Bertram C. Draper, 8511 Bleriot Avenue, Los Angeles, California 90045. Dues are $5.00 for regular members, $1.00 for additional family members and $2.00 for students. Regular members and students receive the annual publication of the Society, *The Echo*.

Executive Board members for the year are: President, Dr. James H. McLean; First Vice-President, Dr. George Radwin; Second Vice-President, Dr. Judith Terry Smith; Secretary, Mrs. Edith Abbott; Treasurer, Mr. Bertram C. Draper; Members at large, Dr. Vida Kenk and Mr. Barry Roth.

AMERICAN MALACOLOGICAL UNION. — The 40th annual meeting of the American Malacological Union will be held in Springfield, Massachusetts, with the Connecticut Valley Shell Club and the Springfield Museum of Science as hosts. Preliminary registration will be held on August 4, 1974. Papers will be presented August 5th through 7th in the auditorium of the Museum of Fine Arts, with some functions at the Museum of Science. A freshwater field trip is planned to a canal which will be drained for easy collecting of mollusks. For further information write to Dr. Harold D. Murray, President, American Malacological Union, Biology Department, Trinity University, San Antonio, Texas 78212, or to Mr. Earl Reed, Springfield Museum of Science, 236 State Street, Springfield, Massachusetts 01103, U.S.A.

UNITAS MALACOLOGICA EUROPAEA. — Fifth European Congress of Malacology and Symposium, September 2-8, 1974, Milan, Italy. The 5th Congress of Unitas Malacologica Europaea will be held in Milan from 2 September 1974 until 8 September 1974 at the Civic Museum of Natural History and at the Hydrobiological Station and Aquarium of the Municipality of Milan. In Milan there are many first and second class hotels in the central areas, whereas the recommendable third-category hotels are situated in very suburban areas. Space in the hostels is very limited, so bookings should be made as early as possible. All the participants who expect to submit papers are asked to send a summary at their earliest convenience. These summaries should be in French, English or German and should not have more than 20 typed lines. The participants will receive a copy of the summaries at the beginning of the Congress. Those interested in participating in the symposium on polymorphism in gastropods should contact Prof. Cesare Sacchi, Institute of Zoology of the University, Piazza Botta, 27100 Pavia, Italy. All other communications should be sent to: Fifth European Congress of Malacology, Civic Museum of Natural History, Corso Venezia 55, Milan.

LERNER MARINE LABORATORY. — The Lerner Marine Laboratory, a field station of The American Museum of Natural History, Central Park West at 79th Street, New York, N.Y. 10024, U.S.A., is issuing an invitation to scientific investigators in the fields of marine biology and botany to make use of its research facilities located at Bimini, Bahamas. Interested scientists and students can obtain more information about the Laboratory by writing to Dr. Jerome G. Rozen, Jr., Deputy Director for Research, The American Museum of Natural History, 79th Street and Central Park West, New York, New York 10024, U.S.A.

VOUCHER SPECIMENS. — The following request for the adoption of editorial guidelines in regard to voucher specimens of mollusks has been sent recently to scientific journals in the United States by Dr. Alan Solem in behalf of the Council of Systematic Malacologists:

The Council of Systematic Malacologists is recommending to the editors of all scientific journals that a prerequisite for publication of a manuscript relating to any aspect of research on mollusks should be the inclusion of a citation as to where voucher specimens of the species involved have been deposited. This is to enable examination by individuals who in the future wish to duplicate or check the results reported.

Repeating an experiment requires duplicating the conditions under which the original procedure was carried out. While virtually all experimental papers today carefully delineate the procedures followed and the methods of data analysis, all too often one critical factor is overlooked. The organism may be cited by name, but only infrequently is the exact locality specified from which the material was obtained, and only rarely are voucher specimens cited as having been placed into a permanent repository. This all too often

means that one of the most important parameters of the initial experiment, the identity of the organisms used, cannot be verified.

The number of living molluscan species is somewhere between 50,000 and 100,000. A relatively small community of systematic workers is attempting to sort out this diversity. As a result, for many groups there has not been a monograph produced in this century and any names which are attached to specimens must be considered tentative and provisional. Under these circumstances the placement of voucher specimens in a collection where they reasonably can be expected to receive permanent housing and care is a necessary and vital aspect of the research process. Such a repository should be a national, private or major university museum collection, preferably one which assigns individual catalog numbers to each set of material. Such numbers should be included in the publication, so that the curator can readily retrieve, in answer to future requests, any material so deposited. Adoption of such a procedure will, in addition, provide a partial check on accuracy of identifications prior to publication. This procedure may actually prevent major errors from being published, and will have the side effect of improving synoptic coverage in molluscan collections.

In addition to contacting journals that are primarily publication outlets for malacological research, we are making this general announcement in hopes of reaching editors of journals that only occasionally publish research reports on mollusks. In the aggregate, well over half of the published molluscan literature each year appears in non-malacological journals. Usually it is these publications that present the most consistent problem in terms of voucher specimen absence. The cooperation of editors and research scientists alike is solicited.

INDEX ANIMALIUM. — Research on an index patterned after C. D. Sherborn's *Index Animalium* is underway at the National Museum of Natural History, Washington, D.C. 20560, U.S.A. The coverage is Mollusca only, and plans are to include original references for names of species and subsequent references to publications including illustrations. The period of chronological coverage begins in 1850, where Sherborn ended, and continues through 1870 to provide an overlap with the *Zoological Record*. Persons having knowledge of or access to obscure pertinent references are invited to correspond with the compiler, Florence A. Ruhoff, Department of Invertebrate Zoology, Mollusks.

EPA MOLLUSK IDENTIFICATION MANUALS. — In 1972 the U.S. Environmental Protection Agency published the first in a series of Identification Manuals on the "Biota of Freshwater Ecosystems," as part of their "Water Pollution Control Research Series." The first of these was on freshwater planarians (Turbellaria), and succeeding publications have dealt with branchiuran crustaceans (*Argulus*), amphipod crustaceans (Gammaridae), isopod crustaceans (Asellidae), polychaete worms (Polychaeta), leeches (Hirudinea), freshwater nematodes (Nematoda), aquatic dryopoid beetles (Coleoptera), and 2 of the series, both written by J. B. Burch, are on mollusks. The 2 mollusk keys are: Identification Manual No. 3 - *Freshwater sphaeriacean clams (Mollusca: Pelecypoda) of North America* and Identification Manual No. 11 - *Freshwater unionacean clams (Mollusca: Pelecypoda) of North America*.

Both of the mollusk publications were prepared with some reservations by the author, since in neither clam group has a completely satisfactory taxonomy been produced, and a key as large and comprehensive as the unionacean mussel key, covering all of North America, had never previously been attempted. Both of the clam groups have nominal species which have been notoriously difficult to identify, largely as a result of past taxonomic splitting and species-naming, and inadequate taxon descriptions. Since modern concepts regarding the nature of the species itself have hardly been applied to freshwater clams, especially in light of critically studied individual and population variation, breeding and cross-breeding potential and ecologically conditioned vs. genetically determined variation, it is difficult to assess accurately what morphological variation might be ascribed to any of the lower taxonomic categories. While it is true that a few apparent clines have been pointed out and certain species seem to have different forms in unusual habitats, definitive studies on such variation are rare or totally lacking. And the higher classification fares no better. How to define families and subfamilies and which genera to put in them is still controversial. Yet, at the lower taxonomic levels, it has been possible for various taxonomists to synonomize a great many nominal species, which made construction of the keys easier. [Exceptions exist, however, and in the genera *Pleurobema* and *Villosa* it is impossible at present to construct a workable key, or to devise a reasonable synonymy for the redundant names.] Another problem that exists is a lack of a universally accepted nomenclature, even for some taxa for which there is little question as to identity or validity. From the beginning of North American malacology, taxonomic nomenclature of freshwater mussels has been the subject of much controversy. Some of the arguments still go on today; at one extreme are those who seem to delight in resurrecting obscure scientific names of doubtful validity, and at the other extreme are those who in apparent ignorance of proper nomenclatural practice stubbornly resist any nomenclatural improvement. So it is sometimes difficult for the non-nomenclaturist to know which is the proper name for some taxa.

Much of the literature on freshwater clams, such as it is, is in generally obscure publications, often inaccessible to the field worker who would most need access to them. For example, the most definitive publication covering North American mussels is Sympson's 1914 *A descriptive catalogue of the naiades or pearly freshwater mussels*, published privately by Bryant Walker (now deceased) in Detroit. In addition to its inaccessibility to many workers, another drawback is its lack of illustrations, which, together with the

relative nature of the taxonomic descriptions, makes it of little practical value to the non-taxonomist. Much of the other literature is regional in nature and is often without adequate illustrations or taxonomic descriptions to help the person who does not have a large museum collection at his disposal.

But, in spite of the many taxonomic uncertainties and the dearth of definitive systematic studies, clams are common in our fresh waters, and those people working on benthic organisms and various other aspects of aquatic biology, including pollution studies, will very often come across them. The clam keys, in spite of their imperfections, were designed for these workers. Because the working systematicists will be revising past taxonomic judgements and improving our knowledge, it is desirable to up-date the clam keys from time to time, and plans are underway to do that. At periodic intervals supplements will be published which will add new knowledge and improvements, call attention to recent revisions, and point out and correct past errors. These supplements to the clam keys will also identify more completely than was possible in the original keys the regional literature references on North American freshwater clams, and will also include synonymies as well as list taxon changes and newly described species.

These keys to North American freshwater invertebrates are available from the U.S. Government Printing Office, Washington, D.C., U.S.A.

COURT CASE TO HALT CONSTRUCTION ON DAMS ON THE DUCK RIVER, TENNESSEE. — In 1972 the Environmental Defense Fund and the Duck River Preservation Association filed suit to prevent construction of the Tennessee Valley Authority's (TVA) Duck River project in Central Tennessee. Entering prominently into the case is the effect of the dams on the freshwater mollusk fauna of the river.

The proposed TVA project consists of 2 dams on the Duck River, one near Columbia and the other near Normandy. Construction began at the Normandy site in 1972. The Duck River is the longest remaining wild river in Central Tennessee, and flows through an unusually beautiful and diverse environment. According to the plaintiffs, the project would inundate wildlife habitat, archaeological and historic sites, fertile farmland, would threaten extinction to certain animal species, and would displace 440 families. The plaintiffs questioned the need for constructing the dams, contending that the dams' economic benefits would barely exceed their costs, and that there are viable alternatives to the project. The case finally came to trial in January, 1974, and the decision of the judge is currently being awaited.

During the trial a Deputy Assistant Secretary of the Department of Interior, Mr. Curtis Bohlen, recommended that construction on the dams be halted to prevent serious threats to the continued existence of several species of freshwater mussels in the Duck River. He cited 9 species and 2 subspecies of mussels as being endangered by the TVA project. But, a TVA witness, Dr. Henry van der Schalie, testified that there are practically no mussels left in the Duck River now and that the project would therefore have little effect on the mussel populations. However, Dr. David H. Stansbery testified for the plaintiffs that the Duck River still has freshwater clams and had one of the richest and most diversified mussel faunas in the world. He said that 90% of the mussel fauna in the river would be eliminated by the TVA project, including 8 species that are rare and endangered.

MOLLUSK SEMINAR AT THE UNIVERSITY OF MICHIGAN, June 1974. — A seminar on various aspects of malacology will be held at the Museum of Zoology, The University of Michigan, 22 June 1974. Areas covered will depend on the participants. The seminar will be informal and will consist of a series of brief presentations by participants followed by brief discussions. More extensive discussions may be arranged in subjects of special interest.

Those wishing to attend or to participate in the seminar should contact Janet White-Rudolph, Museum of Zoology, Mollusk Division, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.

Malacological Review, 1974, 7: 63-64

OBITUARY
GEORGE PAUL KANAKOFF
1897-1973

George Paul Kanakoff died of a respiratory ailment on March 11, 1973, in Los Angeles. To his many friends who knew him fondly as "Uncle George," his passing is a deep personal loss.

Kanakoff was born in Simferopol, Crimea, Russian Empire, on January 18, 1897. He attended Cadet School at Soomy and later went to Paul I Military Academy in Saint Petersburg, where he specialized in artillery and graduated in 1914 as a lieutenant. In 1915, he graduated from Kharkov State University with majors in history and philology, after which he served in the Imperial Army as an artilleryman and took part in heavy fighting during World War I and the Russian Revolution.

Kanakoff immigrated to the United States in November of 1923 and lived in New York for 2 1/2 years. He then moved to Los Angeles and earned a living at a series of occupations. In 1932, he began teaching classes in the Russian language and in the history of the Russian theater, later becoming a professor of Russian at East Los Angeles Junior College. Besides his native Russian, Kanakoff was fluent in Turkish, Tartar, Montenegro and Sart, and competent in German, French, Latin, some Chinese dialects and several Slavic languages. He periodically translated documents for the U.S. Department of State, was for many years the Russian language Editor of *Malacologia*, and published *Soglasiye*, his own monthly Russian-language journal of cultural and political commentary. Kanakoff had a deep and active interest in the theater and played in countless amateur productions since he was 18. His more recent roles were performed with the Russian Theatrical Group of Los Angeles and San Francisco.

Kanakoff's first publication appeared in 1914 as "Ural-Altay word roots in Russian literature of the XVI to XVIII centuries," *Kharkov State Univ. Bull.* 178, and was soon followed by a number of articles in the Russian military journal *Heavy Artillery*. His first publication in America, in 1924, was "A rare manuscript of Kurdistan, late Fifteenth Century, in the collection of the New York Public Library," *Publs. Philol.*, Columbia Univ., New York.

Because of his interest in natural history, Kanakoff worked as a volunteer assistant at the Los Angeles County Museum, beginning in 1935. He became a permanent employee of the Zoology Section in 1937 and began to specialize in mollusks. Following the death of George Willett, Kanakoff was appointed Curator of Invertebrate Paleontology in January, 1948, and occupied that position until his retirement in 1966. After retirement, he served as 1/2-time curator for 1 year and continued to work in his spare time at the museum on research projects until shortly before his death. Kanakoff was Past-President of the Conchological Club of Southern California and served for nearly 20 years as sponsor of the club's meetings at the museum.

Kanakoff began publishing scientific works in 1939 and produced a number of papers in biology and molluscan paleontology. His principal interest was in late Cenozoic mollusks of southern California, and he was a consummate collector, spending much of his time in the field. With an ever-changing retinue of eager student assistants, he amassed enormous collections, especially from the late Pleistocene Palos Verdes Formation and the Pliocene San Diego Formation. His standing orders to "save everything" in the field and laboratory have made his collections a rich source of specimens for both molluscan and non-molluscan specialists. His largest published work is "Late Pleistocene invertebrates of the Newport Bay area, California," co-authored with William K. Emerson (1959, *Contr. Sci., Los Angeles Co. Mus.*, 31: 1-47). A number of publications by other workers are based on specimens he collected.

Kanakoff took especial delight in teaching weekly paleontology classes each spring to high school students at the museum, because these eager recruits provided labor for his many collecting trips. His excellence as a collector and his light-hearted approach to life were qualities we students could only imperfectly emulate.

The most pleasant and enduring memories of George Kanakoff belong to those of us who served as his field and laboratory assistants. He was our beloved "Uncle George," and we were his devoted "slaves," collecting and sorting fossils with an eagerness and interest he instilled in us. Uncle George was a colorful, cultured and amusing man, and his passing leaves us devoid of a friend and inspiring soul.

LOUIE MARINCOVICH

Malacological Review, 1974, 7: 65-92

CONTENTS OF CURRENT SERIAL PUBLICATIONS ON MOLLUSKS

The contents of current malacological serial publications, as shown by their tables of contents, are herewith reproduced as a service to the scientific community. The journals are listed in alphabetical order. Also listed are the locations of the editorial offices. Those publications that do not have their contents printed in this current issue of *Malacological Review* (Vol. 7, No. 1) are marked by an asterisk in the right hand column below; contents of these publications will be included in future issues of *Malacological Review*.

Journal	Location of Editorial Office	Page
The American Malacological Union, Inc., Bulletin	Ottawa, Canada	*
Archiv für Molluskenkunde	Frankfurt-am-Main, Germany (FR)	66
Argamon	Jerusalem, Israel	67
Basteria	Leiden, The Netherlands	*
Comunicaciones de la Sociedad Malacológica del Uruguay	Montevideo, Uruguay	69
Conchiglie	Milano, Italy	70
The Echo	San Francisco, Calif., U.S.A.	*
Gastropodia	Fleetwood, Pa., U.S.A.	*
Haliotis	Paris, France	*
Johnsonia	Cambridge, Mass., U.S.A.	*
Journal de Conchyliologie	Mosman, N.S.W., Australia	71
Journal of Conchology	Bromborough, Cheshire, U.K.	72
Journal of the Malacological Society of Australia	Geelong, Vict., Australia	*
Lavori della Società Malacologica Italiana	Milano, Italy	73
Malacologia	Ann Arbor, Mich., U.S.A.**	74
Malacological Review	Whitmore Lake, Mich., U.S.A.	81
Malakologische Abhandlungen	Dresden, Germany (DR)	*
The Nautilus	Greenville, Dela., U.S.A.	82
Occasional Papers on Mollusks	Cambridge, Mass., U.S.A.	*
Proceedings of the Malacological Society of London	Reading, U.K.	83
Proceedings of the National Shellfisheries Association	Oxford, Md., U.S.A.	*
Soosiana	Baja, Hungary	*
Sterkiana	Columbus, Ohio, U.S.A.	*
The Veliger	Berkeley, Calif., U.S.A.	85
Venus	Tokyo, Japan	*

**To change to Philadelphia, Pa., U.S.A., beginning with Vol. 15, 1974.

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der Senckenbergischen Naturforschenden Gesellschaft
Organ der Deutschen Malakozoologischen Gesellschaft

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Weitergeführt von Dr. W. Wenz und Dr. F. Haas
Herausgegeben von Dr. A. Zilch

Band 103 Nummer 1/3

Inhalt.

Schütt, H. & Besenecker, H.: Eine Molluskenfauna aus dem Neogen von Chios (Ägäis). (Tafel 1-2). 1

Kadolsky, D.: Die vorpliozänen Littorinidae und Lacunidae Mitteleuropas (Gastropoda: Prosobranchia). 31

Nordsieck, H.: Zur Anatomie und Systematik der Clausilien, XII. Phaedusinae, I: Phaedusen aus Nepal und ihre systematische Stellung innerhalb der Unterfamilie. (Tafel 3). 63

Grossu, A. V. & Tesio, C.: Revision der Arten der Alopiinae aus den südlichen Karpathen nebst Beschreibung einer neuen Art (Gastropoda: Clausiliidae) 87

Brabenec, J.: Ein Beitrag zur Verbreitung der Alpenclausiliide *Iphigena badia crispulata* (Westerlund). 93

Pintér, L. & Szigethy, A.: Über zwei *Acicula*-Arten aus Jugoslawien (Gastropoda: Prosobranchia). 97

Zilch, A.: Die Typen und Typoide des Natur-Museums Senckenberg, 51: Mollusca: Achatinacea (2): Ferrussaciidae, Subulinidae. (Tafel 4-5). 99

Frankfurt am Main 1973

Arch. Moll. | 103 | (1/3) | 1—152 | Frankfurt a. M., 3. 9. 1973

ARGAMON

JOURNAL OF
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Vol. 3, No. 1-4, 1972

Editor Argamon: H.K. Mienis
Editors Argamanit: Z. Bar & I. Yaron

CONTENTS

Page

Foin, T.C., and L.P. Ruebush: A note on new *Cypraea* in the Southern Red Sea 1

Yaron, I.: Book review (Parenzan) 4

Foin, T.C.: The Zoogeography of the Cypraeidae in the Red Sea Basin . . 5

Mienis, H.K.: On the nomenclature and distribution of *Columbella savigny* (Gastropoda, Columbellidae) 17

Mienis, H.K.: Nomenclatural note on *Naytia obliqua* (Kiener) (Gastropoda, Nassariidae 20

Mienis, H.K.: Cypraeidae from the Sinai Area of the Red Sea. 2: Two additional species: *Palmadusta microdon chrysalis* (Kiener) and *Bistolida teres* (Gmelin), with notes on other species 21

Mienis, H.K.: Additions to the checklist of Terebridae from the northern part of the Red Sea 27

Yaron, I.: Further additions to the Mediterranean molluscan fauna of Israel 33

Foin, T.C. and D.T. Bosch: Analysis of *Cypraea grayana* Schilder, 1930 . . 37

Yaron, I.: Book review (Furlong & Pill) 50

Morrison, J.P.E.: Mediterranean *Siphonaria:* West and East – Old and New 51

Wolda, H.: Changes in shell size in some experimental populations of the landsnail *Cepaea nemoralis* (Linnaeus) 63

Yaron, I.: Book review (McLean) 72

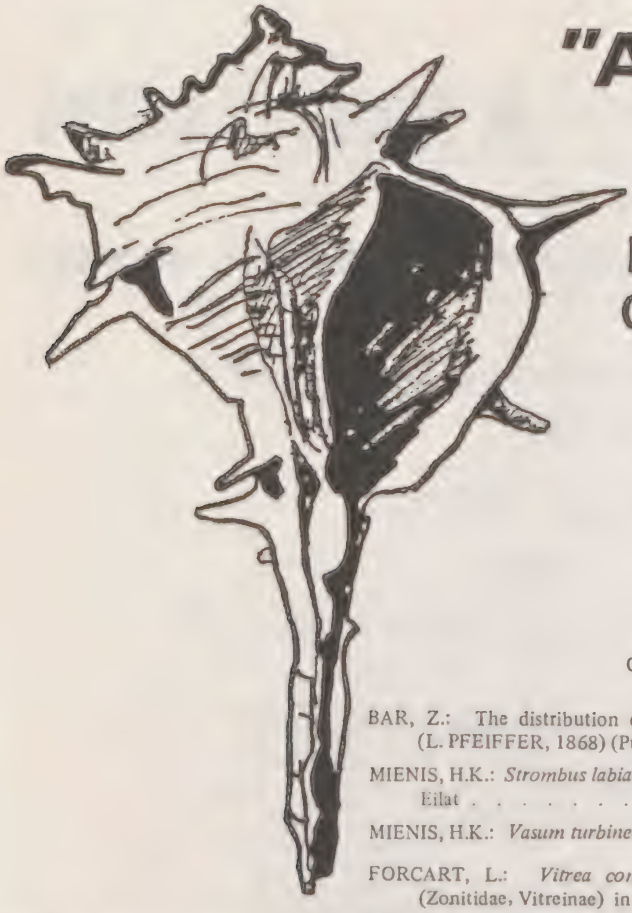
Notes – News – Information

Lazar, D.: The Malacological Museum of the Nahariya Municipality 73

Research requests 75

Mienis, H.K., and Z. Bar: Recent publications concerning our region 75

Contents 78



"ARGAMON"

ISRAEL JOURNAL OF MALACOLOGY

Volume 4, No. 1

CONTENTS

	Page
BAR, Z.: The distribution of *Jaminia (Euchondrus) ledereri* (L. PFEIFFER, 1868) (Pulmonata, Enidae)	1
MIENIS, H.K.: *Strombus labiatus* and *Strombus aurisdianae* from Eilat	6
MIENIS, H.K.: *Vasum turbinellus* from the Mediterranean	6
FORCART, L.: *Vitrea contracta* (WESTERLUND, 1873) (Zonitidae, Vitreinae) in Palestine	7
MIENIS, H.K.: *Eobania vermiculata* (MULLER) in Israel (Gastropoda, Helicidae)	9
COOMANS, H.E.: Additional notes on the genus *Pachybathron* (Gastropoda, Marginellidae)	11
YARON, I.: A note on the taxonomic status of *Chiton affinis* ISSEL	15
MIENIS, H.K.: A bivalved gastropod from Eilat	18
MIENIS, H.K.: A first record of Omalogyridae from the Mediterranean coast of Israel	18
MIENIS, H.K.: Note on *Gregariella petagnae* (Scacchi) (Pelecypoda, Mytilidae)	19
MIENIS, H.K.: Notes on recent and fossil Neritidae 4, *Nerita lineata* GMELIN, 1791, a junior homonym of *Nerita lineata* MULLER, 1774	21
MIENIS, H.K., and Z. BAR: Recent publications concerning our region	23

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Vol. III - Nº 22 Abril de 1972

S U M A R I O

Pág.

FARIA VAZ, Jorge - Sobre la presencia de Periploma ovata d'Orbigny, 1846 (Bivalvia, Periplomatidae), en el litoral de São Paulo, Brasil..... 167

FIGUEIRAS, Alfredo y SICARDI, Omar E. - Catálogo de los Moluscos Marinos del Uruguay. Parte VII..... 169

DUARTE, Eliseo - Notas de Secretaría..... 189

Vol. III - Nºs 23 - 24 Octubre 1972 - Abril 1973

S U M A R I O

Pág.

RIOS, E. C. - Moluscos marinos de la Expedición Geomar IV 193

FIGUEIRAS, Alfredo y BROGGI, Jorge - Estado actual de nuestros conocimientos sobre los moluscos fósiles del Uruguay (Parte III - Cont.) 203

SICARDI, Omar E. - Estudio preliminar sobre Adelomelon martensi (STREBEL, 1906) 241

DUARTE, Eliseo - Notas de Secretaría 246

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Conchiglie

NOTIZIARIO MENSILE
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ADERENTE ALLA
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Anno VIII - n. 11-12 novembre-dicembre 1972

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CATALOGO ILLUSTRATO DELLE CONCHIGLIE MARINE DEL MEDITERRANEO

4

Anno IX - n. 1-2 gennaio-febbraio 1973

PANETTA P. - *Lepetella laterecompressa* (De Rayn. & Ponzi) . . . . . pag. 1

CAPROTTI E. - Esempi di migrazioni e di evoluzione di molluschi neogenici mediterranei . » 7

FRANCHINI D. - Note sulla bioecologia di una rilevante popolazione di *Coralliophila babelis* . » 17

GHISOTTI F. - Metodi e Tecniche: dispositivo per osservare e fotografare piccoli molluschi » 20

SPADA G. - Rinvenimenti malacologici nel Mediterraneo . . . . . » 22

Recensioni e segnalazioni bibliografiche . . . . . » 25

Glossario . . . . . » 27

Anno IX - n. 3-4 marzo-aprile 1973

SPADA G. - SABELLI B. - MORANDI V. - Contributo alla conoscenza della malacofauna dell'isola di Lampedusa . . . . . pag. 29

GHISOTTI F. - *Scapharca* cfr *cornea* (Reeve), ospite nuova del Mediterraneo . . . . . » 68

Nelle pagine centrali il 3° e 4° inserto della GUIDA PRATICA ALLA FORMAZIONE DI UNA RACCOLTA DI CONCHIGLIE MARINE di **Gianni Spada.**

Anno IX - n. 5-6 maggio-giugno 1973

DI GERONIMO I. - PANETTA P. - La Malacofauna Batiale del Golfo di Taranto . . . . . pag. 69

FRANCHINI D.A. - *Trophonopsis (Pagodula) vaginata* (Jan, 1832) ha validità nei confronti del *taxon T. (P.) carinata* (Bivona pt., 1832) . . . . . » 123

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JOURNAL
DE
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TABLE DES MATIERES

Vol. CX, No. 1 Paru le 20 décembre 1972

PAGES

Intérêt taxonomique de l'electrophorèse sur cellogel RS des protéines solubles de la partie transparente du muscle adducteur de cinq espèces d' *Ostreidae*, par P. MORÉ, M. T. MORÉ, R. MONNET, J. POISBEAU et F. TAUNAY 3

La notion de pleurothétie et l' organisation des Hippurites, par Gaston ASTRE 9

The Identity of *Conus spirogloxus* Deshayes, by A. B. JENNER 17

Récolte de Mollusques Lamellibranches sur la côte du Cambodge, par P.-H. FISCHER et E. FISCHER-PIETTE 22

Nécrologie: Gilbert Ranson, par E. Fischer-Piette 31

Bibliographie 32

Vol. CX, No. 2 Paru le 30 mai 1973

PAGES

The types of *Unionidae* (Mollusca: Bivalvia) described by C. S. Rafinesque in the Museum National d'histoire naturelle, Paris, by Richard I. JOHNSON 35

Observations d'écologie littorale à Punta Arenas (Chili), par P.-H. FISCHER et E. FISCHER-PIETTE 38

Les Mollusques testacés du Cambodge - Première partie: Introduction et Gastéropodes Prosobranches, par P.-H. FISCHER 40

Variétés. Figurations de Mollusques sur des timbres-poste, par P.-H. FISCHER 65

Propositions faites au Bulletin of Zoological Nomenclature 68

Nouvelles: La Collection de Charles Mayer-Eymar, par le Dr. Peter JUNG 68

Nécrologie: Alice Pruvot-Fol, Tom Iredale 69

Bibliographie 70

Pour toute communication scientifique ou souscription aux volumes en cours, s'adresser à M. P.-H. FISCHER, directeur du Journal, 18/55 Prince Albert Str., Mosman, N.S.W. 2088, Australie.

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Vol. 28 No. 1 May, 1973

PAGE

D. Heppell—Two historical '*Pinna ingens* Pennant' in the Royal Scottish Museum. 1

A. Gautier—A note on Hudi Chert fresh-water molluscs with description of *Lanistes grabhami* Cox 1933 from Hanakat el Kuleiwat (Sudan). .. 5

J. X. Corgan—The names *Partulida* Schaufuss, 1869 and *Spiralinella* Chaster, 1901.' 9

A. C. van Bruggen—*Lauria cylindracea* and *Granopupa granum* to be removed from the South African list. 11

B. W. Barrett and J. E. Chatfield—*Discus rotundatus* (Müller) growing on algae. 13

F. G. Berry—Patterns of snail distribution at Ham Street Woods National Nature Reserve, E. Kent. 23

D. M. Duval—Note on acceptability of various weeds as food for *Arion hortensis* Férussac. 37

R. N. Brehaut—Occurrence of *Charonia lampas* (L.) at Guernsey. .. 41

M. J. and S. J. Bishop—Associations of molluscs and marine plants at San Diego, California. 43

Reviews 4, 22, 55, 58, 59

Nora F. McMillan—A rare "Sowerby" leaflet 40

Vol. 28 No. 2 October, 1973

PAGE

T. E. Crowley—Fictional Mollusca 61

T. E. Thompson—Protective resemblances in British *Lamellaria* 75

D. S. Brown—The Palaearctic element in late Quaternary lake faunas of Southern Ethiopia 79

T. E. Crowley, J. R. Green and N. F. McMillan—Some Mollusca from Northern Nigeria 81

R. G. Meiklejohn—A list of Caithness land and freshwater Mollusca ... 95

J. G. Evans and Hilary Jones—Subfossil and modern land-snail faunas from rock-rubble habitats 103

Obituary—H. E. J. Biggs 131

Reviews 102, 130

LAVORI
della
Società Malacologica Italiana

Volume IX

Segretario: Ferdinando Toffoletto
Direttore della Rivista: Fernando Ghisotti
Bibliotecario: Gianfranco Sacchetti

SOMMARIO

Società Malacologica Italiana . . . . . pag. II
Modifiche allo Statuto e deliberazioni dell'Assemblea e del Consiglio Direttivo . . . . . » IV
Elenco dei Soci al 31 Dicembre 1972 . . . . . » V
Attività della Società Malacologica Italiana . . . . » VIII

LAVORI

1. Barbato G.: Studio sul comportamento stagionale di *Viviparus ater* (Crist. & Jan) dei laghi d'Iseo e di Garda (*Gastropoda Viviparidae*).
2. Barsotti G. & Frilli G.: Contributo alla conoscenza della macofauna dei fondi sublitorali dell'alto Tirreno (Mare toscano).
3. Boldori L.: Corrado Allegretti. Una fiamma s'è spenta nelle grotte bresciane (25.2.1894 - 2.5.1969).
4. Giusti F.: Notulae malacologicae. X *Testacelloides* Wagner e *Testacella* (*Testacelloides*) *gestroi* Issel, un buon sottogenere ed una buona specie della Sardegna.
5. Giusti F.: Notulae malacologicae. XI. Alcune nuove specie di molluschi terrestri dell'isola di Sardegna.
6. Giusti F. & Mazzini M.: Notulae malacologicae XIV. I molluschi delle Alpi Apuane. Elenco delle specie viventi con descrizione di una nuova specie: *Vitrinobrachium baccettii* n. sp.
7. Levi-Setti F. & Pinna G.: *Platystrophites*, nuovo genere nella serie toarciana ad ammoniti del Passo del Furlo (Pesaro) (*Ammonoidea Dactylioceratidae*).
8. Pinna G.: I tipi delle specie di Gasteropodi terziari istituite da Giuseppe De Cristofori e Giorgio Jan nel 1832 conservati nelle collezioni del Museo Civico di Storia Naturale di Milano.
9. Toffoletto F.: Il primo Congresso della Società Francese di Malacologia.
10. Toffoletto F.: Il IV Congresso dell'Unitas Malacologica Europaea.
11. ———: Il Simposio sull'« Importanza dei Molluschi nel problema degli inquinamenti » Ispra, 30-XI-1969.

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Vol. 12, No. 1 **MALACOLOGIA** 1973

CONTENTS

R. H. POHLO

Feeding and associated functional morphology in *Tagelus californianus* and *Florimetis obesa* (Bivalvia: Tellinacea) 1

E. G. DRISCOLL and D. E. BRANDON

Mollusc-sediment relationships in northwestern Buzzards Bay, Massachusetts, U.S.A. 13

M. CASTAGNA and P. CHANLEY

Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western Midatlantic coast 47

M. J. IMLAY

Effects of potassium on survival and distribution of freshwater mussels 97

G. WIUM-ANDERSEN

Electrophoretic studies on esterases of some African *Biomphalaria* spp. (Planorbidae) 115

E. S. DEMIAN and F. YOUSIF

Embryonic development and organogenesis in the snail *Marisa cornuarietis* (Mesogastropoda: Ampullariidae)
I. General outlines of development 123

E. S. DEMIAN and F. YOUSIF

Embryonic development and organogenesis in the snail *Marisa cornuarietis* (Mesogastropoda: Ampullariidae)
II. Development of the alimentary system 151

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MALACOLOGIA

Vol. 12, No. 2 1973

CONTENTS

E. S. DEMIAN and F. YOUSIF

Embryonic development and organogenesis in the snail *Marisa cornuarietis* (Mesogastropoda: Ampullariidae). III. Development of the circulatory and renal systems 175

E. S. DEMIAN and F. YOUSIF

Embryonic development and organogenesis in the snail *Marisa cornuarietis* (Mesogastropoda: Ampullariidae). IV. Development of the shell gland, mantle and respiratory organs 195

J. N. CATHER

Regulation of apical cilia development by the polar lobe of *Ilyanassa* (Gastropoda: Nassariidae) 213

M. L. M. LE PENNEC

Morphogenèse de la charnière chez 5 espèces de Veneriidae. 225

M. R. CARRIKER and H. H. CHAUNCEY

Effect of carbonic anhydrase inhibition on shell penetration by the muricid gastropod *Urosalpinx cinerea* 247

B. MORTON

Some aspects of the biology and functional morphology of the organs of feeding and digestion of *Limnoperna fortunei* (Dunker) (Bivalvia: Mytilacea) 265

S. K. PIERCE

The rectum of *"Modiolus" demissus* (Dillwyn) (Bivalvia: Mytilidae): A clue to solving a troubled taxonomy 283

W. F. PONDER

The origin and evolution of the Neogastropoda 295

E. FISCHER-PIETTE and D. VUKADINOVIC

Sur les mollusques fluviatiles de Madagascar. 339

P. T. CLAMPITT

Substratum as a factor in the distribution of pulmonate snails in Douglas Lake, Michigan 379

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MALACOLOGIA

CONTENTS

FOURTH EUROPEAN MALACOLOGICAL CONGRESS

Preface . . . . . *iii*
Introduction 1
Allocution présidentielle 3
Presidential address, English summary 4
Anrede des Vorsitzenden, Deutsche Zusammenfassung 5
Report on the General Assembly of UNITAS MALACOLOGICA EUROPAEA 7
Compte-rendu de l'Assemblée générale de l'U.M.E. 9
Bericht über die Generalversammlung der U.M.E. 11
Compte-rendu de la réunion de Faunistique continentale, le 10 septembre 1971 . . . 13
Working Conference on Distribution Mapping, September 10th, 1971 14
Malacologists and the protection of Molluscs 15
Resolution by UNITAS MALACOLOGICA EUROPAEA on the protection of Molluscs. . 16

Paleontology

ADEGOKE, O. S.: Paleocene Mollusks from Ewekoro, Southern Nigeria. 19
KROLOPP, E.: Faunengeschichtliche Bedeutung der altpleistozänen Molluskenfauna von Ungarn 29
NORTON, P. E. P. & SPAINK, G.: The earliest occurrence of *Macoma balthica* (L) as a fossil in the North Sea deposit 33
SPAINK, G.: Phylogenetical investigations in the Neogene Astartidae of the Southern North Sea basin (abstract). 38

Shell structure and Ca secretion

ADEGOKE, O. S.: Mineralogy and biogeochemistry of calcareous operculi and shells of some Gastropods 39
VOVELLE, J.: Transfert du Calcium à travers l'épithélium du repli operculaire chez *Astrea rugosa* L. (Turbinidae). 47
TIMMERMANS, L. P. M.: Mantle activity following shell injury in the pond snail *Lymnaea stagnalis* L. 53

Physiology and Endocrinology

MORTON, B.: A new theory of feeding and digestion in the filter-feeding Lamellibranchia 63
PRINSLOO, J. F. & VAN EEDEN, J. A.: The influence of temperature on the growth rate of *Bulinus* (*Bulinus*) *tropicus* (Krauss) and *Lymnaea natalensis* Krauss (Mollusca: Basommatophora) 81
NEWELL, P. F. & SKELDING, J. M.: Studies on the permeability of the septate junction in the kidney of *Helix pomatia* L. 89
SKELDING, J. M.: Studies on the renal physiology of *Achatina achatina* (L.). . . . 93
OSBORNE, N. N.: Micro-biochemical and physiological studies on an identified serotonergic neuron in the snail *Helix pomatia* 97
FOULQUIER, L., BOVARD, P. & GRAUBY, A.: Résultats expérimentaux sur la fixation du Zinc-65 par *Anodonta cygnea* (L). 107
BORAY, J. C.: The role of the relative susceptibility of snails to infection with helminths and of the adaptation of the parasites in the epidemiology of some helminthic diseases 125
TARDY, J.: Incidence de la castration chirurgicale sur le tractus génital et la ponte chez les Aeolidiidae: Application à la compréhension des mécanismes du contrôle endocrine de la sexualité 129
RUNHAM, N. W., BAILEY, T. G. & LARYEA, A. A.: Studies of the endocrine control of the reproductive tract of the grey field slug *Agriolimax reticulatus* 135

Structure

RIGBY, J. E.: The anatomy of *Cavolinia inflexa* (Pteropoda) (abstract) 143
ALLEN, J. A.: Functional morphology of the Verticordiidae (Bivalvia) (abstract) 143
SOLEM, A.: Convergent evolution in Pulmonate radulae (abstract) 144

PROC. FOURTH EUROP. MALAC. CONGR.

CONTENTS (Continued)

THOMPSON, T. E. & BEBBINGTON, A.: Scanning electron microscope studies of Gastropod radulae 147
SCHELTEMA, A. H.: The radula of the Chaetodermatidae (Aplacophora, Chaetodermatida) (abstract) 166
THOMPSON, T. E.: Euthyneuran and other molluscan spermatozoa 167
SCHMEKEL, L.: Artcharakteristische Feinstrukturen bei Nudibranchiern 207

Systematics of higher categories

ROBERTSON, R.: The biology of the Architectonicidae, Gastropods combining Prosobranch and Opisthobranch traits 215
BURCH, J. B.: A comparative study of some Polish and American Lymnaeidae: an assessment of phylogenetic characters (abstract) 221
SMITH, B. J.: Problems of generic placement in Australian land molluscs (abstract) 222

Systematics of species

RUSSELL, P. J. C. & PETERSEN, G. H.: The use of ecological data in the elucidation of some shallow water European *Cardium* species. 223
PETERSEN, G. H. & RUSSELL, P. J. C.: The nomenclature and classification of some European shallow-water *Cardium* species (abstract) 233
DE ROOIJ-SCHUILING, L. A.: A preliminary report on systematics and distribution of the genus *Ervilia* Turton, 1822 (Mesodesmatidae, Bivalvia). . . 235
STARMÜHLNER, F.: Die Gattung *Melanopsis* Ferussac 1807 auf Neukaledonien. . 242
SABELLI, B.: On a Polyplacophora described by Monterosato (abstract). 244
PARODIZ, J. J.: The species complex of *Diplodon delodontus* (Lam.) (Unionacea - Hyriidae). 247
BOETERS, H. D.: Die Gattung *Bythinella* und die Gattung *Marstoniopsis* in Westeuropa, Westeuropäische Hydrobiidae, 4. (Prosobranchia). 271
WIUM-ANDERSEN, G.: Electrophoresis as a support for the identification of various African *Biomphalaria*. 287
GIUSTI, F.: The minute shell structure of the glochidium of some species of the genera *Unio*, *Potomida* and *Anodonta* (Bivalvia, Unionacea). 291
PEAKE, J. F.: Species isolation in sympatric populations of the genus *Diplommatina* (Gastropoda, Prosobranchia, Cyclophoridae, Diplommatininae). . 303

Systematics: variability, polymorphism

REAL, G.: Polymorphisme du test de *Potamopyrgus jenkinsi* (E. A. Smith, 1889) en milieu saumâtre ou lacustre 313
COOMANS, H. E.: Conidae with smooth and granulated shells. 321
GOODHART, C. B.: A 16-year survey of *Cepaea* on the Hundred Foot Bank. . . . 327
GUERRUCCI, M. A.: Aspects généraux du polymorphisme de la couleur du péristome chez les *Cepaea hortensis* en France 333
PETTITT, C.: An examination of the distribution of shell pattern in *Littorina saxatilis* (Olivi) with particular regard to the possibility of visual selection in this species 339
REX, M. A.: Prediction of the number of color morphs in populations of *Liguus fasciatus* (abstract) 344

Ecology, Ecophysiology

KLEEMANN, K.: *Lithophaga lithophaga* (L.) (Bivalvia) in different limestone. . . 345
SAMPAIO XAVIER, M., DE AZEVEDO, J. F. & MATTOS DOS SANTOS, M.A.: Studies on the distribution and ecology of *Lymnaea truncatula*, intermediate host of *Fasciola hepatica* in Portugal (abstract) 348
VAN DER SCHALIE, H. & BERRY, E. G.: The role of temperature in the ecology and distribution of the snail, *Lymnaea stagnalis* (abstract) 348
BÁBA, K.: Wassermollusken-Zönosen in den Moorwäldern *Alnion glutinosae* (Malcuit) der Ungarischen Tiefebene 349
CAMERON, R. A. D.: Some woodland mollusc faunas from Southern England. . . 355
EDMUNDS, J. & EDMUNDS, M.: Preliminary report on the Mollusca of the benthic communities off Tema, Ghana 371
TRUEMAN, E. R., BLATCHFORD, J. G., JONES, H. D. & LOWE, G. A.: Recordings of the heart rate and activity of molluscs in their natural habitat. . 377
GARCIA, M. C.: Recherches sur l'échauffement de *Cepaea nemoralis* (L.) par l'énergie rayonnée 385
CHATFIELD, J. E.: Aspects of feeding and growth in land snails 391

PROC. FOURTH EUROP. MALAC. CONGR.

CONTENTS (Continued)

IMHOF, G.: Der Einfluss von Temperatur und Photoperiode auf den Lebenszyklus einiger Süsswasserpulmonaten (abstract) 393
MCDONALD, S. C.: Activity patterns of *Lymnaea stagnalis* (L.) in relation to temperature conditions: a preliminary study (abstract) 395

Biogeography

SOLEM, A.: Island size and species diversity in Pacific Island land snails. 397
BARBOSA, F. S.: Possible competitive displacement and evidence of hybridization between two Brazilian species of planorbid snails 401
SCHELTEMA, R. S.: Eastward and westward dispersal of tropical Prosobranch larvae across the Mid-Atlantic barrier (abstract) 409
VALOVIRTA, I.: The distribution of the land molluscs in the upheaval area in the Quarken, an archipelago in the Gulf of Bothnia (summary) 409

Zoogeography

HEATH, J.: The European Invertebrate survey 411
ANT, H.: Vorschläge zur Erfassung der mitteleuropäischen Mollusken (Zusammenfassung) 414
JAYET, A.: Sur quelques Pisidiums haut-alpins 415
VAN BRUGGEN, A. C.: Distribution patterns of the genus *Gulella* (Gastropoda pulmonata: Streptaxidae) in Southern Africa 419
GITTENBERGER, E.: Die Formen von *Abida secale* (Draparnaud) in den östlichen Pyrenäen (Zusammenfassung) 426
MORRISON, J. P. E.: Zoogeography of the pleurocerine fresh water snails (abstract) 426
MEAD, A. R.: A prognosis in the spread of the giant African snail to continental United States (abstract) 427
SALVAT, B.: Mollusques des îles Tubuai (Australes, Polynésie) Comparaisons avec les îles de la Société et des Tuamotu 429
KNUDSEN, J.: Some aspects of the distribution of the marine molluscs of West Africa (abstract) 431
PANETTA, P.: Les mollusques bathyals du Golfe de Tarente (résumé). 432

Miscellaneous

CHAIX, L.: Quelques cas de diphyoidie observés sur des Mollusques continentaux 433
OBERLING, J. J.: Notes on the ornamentation of mollusk shells (abstract). 438
DEMIAN, E. S. & KAMEL, E. G.: Effect of *Marisa cornuarietis* on *Bulinus truncatus* populations under semi-field conditions in Egypt (abstract) 439
GODAN, D.: Die ökologischen Grundlagen der Prüfungsmethoden von Molluskiziden (Zusammenfassung) 439
KO BUN HIAN: A new injection fluid for malacologists (summary) 440
DEXTER, R. W.: Historical aspects of Alpheus Hyatt's work on fossil Cephalopods (summary) 441

Exhibits 445
List of Congress members 447
Index 453

MALACOLOGIA

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VOLUME 6, Number 2 1973

CONTENTS

Research Articles

Fusconaia masoni (Conrad 1834) (Bivalvia: Unionacea) in the Atlantic drainage of the southeastern United States. S. L. H. FULLER 105
Pseudoskenella depressa gen. et sp. nov., an ectoparasite on *Galeolaria*. W. F. PONDER 119
Fecal pellets of *Biomphalaria glabrata*. C. S. RICHARDS. 125
Inherited variability in the course of the intestine in *Biomphalaria glabrata*. C. S. RICHARDS 133

Symposium: Genetics, cytogenetics and hybridization of mollusks. Convener, J. B. BURCH 139

Cytogenetics of gastropod mollusks. C. M. PATTERSON 141
Oyster genetics and the probable future role of genetics in oyster culture. A. C. LONGWELL and S. S. STILES 151
Hybridization in oysters (*Crassostrea*). R. W. MENZEL 179
Oncomelania hupensis (Gastropoda: Hydrobiidae) - hybridization, genetics and transmission of *Schistosoma japonicum*. G. M. DAVIS & M. D. RUFF. . 181
Genetics of *Biomphalaria glabrata* (Gastropoda: Planorbidae). C. S. RICHARDS. 199
Cross-breeding experiments with the African snail genus *Bulinus* (Gastropoda: Planorbidae). S. K. WU 203

Miscellanea

Malacological Review - six years of publication. J. B. BURCH. 207

News and Announcements

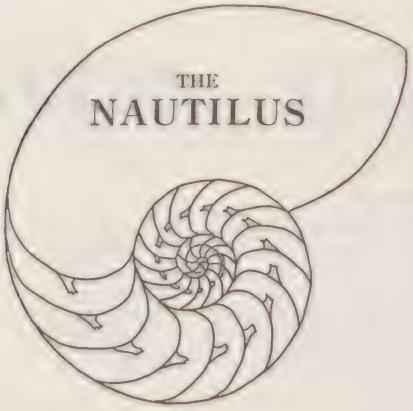
Conchological Society of Great Britain and Ireland, Program of Meetings for 1973 209
Malacological Symposium, Australia. 209
American Malacological Union, 39th Annual Meeting 210
Mollusk Seminar, Ann Arbor 210
The First Asian Malacological Symposium, Hong Kong 211
Colloquium on Molluscan Phylogeny, London. 211
Supplement 1, *Malacological Review - Freshwater Snails of Taiwan (Formosa)*. 211

Book Review

The mollusks of the arid southwest with an Arizona checklist, reviewed by C. M. PATTERSON 213

Contents of Current Malacological Periodicals 215
Author index for malacological periodicals. 238

Index 245



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Volume 87, number 2 -- April 1973

CONTENTS

Thomas R. Waller
The Habits and Habitats of Some Bermudian Marine Mollusks 31

Richard Edward Young
Evidence for Spawning by *Gonatus* sp. (Cephalopoda: Teuthoidea) in the High Arctic Ocean 53

S. L. H. Fuller and C. E. Powell, Jr.
Range Extensions of *Corbicula manilensis* (Philippi) in the Atlantic Drainage of the United States..59

Margaret C. Teskey
Emarginula dentigera Heilprin, 1889, a Littoral Mollusk 60

Book Reviews
(of) S. Peter Dance, 52; A. Myra Keen, 58

News; AMU Meeting in June 1973 .....59, 60

Volume 87, number 3 – July 1973

CONTENTS

Ronald F. Thomas and Lee Opresko
Observations on *Octopus joubini:* Four Laboratory Reared Generations 61

Dorothea S. Franzen
Oxyloma deprimida, a New Species of Succineidae (Pulmonata) 66

David Nicol and Graig D. Shaak
Late Eocene Distribution of the Pelecypod *Exputens* in Southeastern United States 72

John N. Kraeuter
Notes on Mollusks *Ostrea* and *Siphonaria* from Georgia (U.S.A.) 75

Maria Luiza S. Mello and Marlene T. Ueta
Observations by Polarized Light on the Radula of *Aplexa marmorata* 79

Alan K. Craig
A New Record for *Liguus:* The Boynton Beach Colony 83

Stuart A. Harris
Pisidium henslowanum (Sheppard) in Western Canada 86

James T. Carlton
Corbicula in San Francisco, California 87

Robert Robertson
Cyclostremella: A Planispiral Pyramidellid 88

Donald R. Shasky
Obituary of G. Bruce Campbell, M.D. 89

Frank Perron and Thomas Probert
Viviparus malleatus in New Hampshire 90

Book Reviews
(of) Tom Rice, 77; J. C. Bequaert and W. B. Miller, 78; Recent Publications, 74.

VOLUME 40 · PART 4 · APRIL 1973

PROCEEDINGS OF THE Malacological Society OF LONDON

EDITED BY A. GRAHAM D.Sc.
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Publication Committee

CONTENTS

T. E. THOMPSON. Sacoglossan gastropod molluscs from Eastern Australia 239

R. S. K. BARNES, J. COUGHLAN and N. J. HOLMES. A preliminary survey of the macroscopic bottom fauna of The Solent, with particular reference to *Crepidula fornicata* and *Ostrea edulis* 253

G. MANDAHL-BARTH. Descriptions of new species of African freshwater molluscs 277

D. S. BROWN and G. MANDAHL-BARTH. Two new genera of Planorbidae from Africa and Madagascar 287

RONALD F. THOMAS. Homing behavior and movement rhythms in the pulmonate limpet, *Siphonaria pectinata* Linnaeus 303

GAMIL N. SOLIMAN. On the structure and behaviour of the rock-boring bivalve *Rocellaria retzii* (Deshayes) from the Red Sea 313

J. H. CROTHERS. On variation in *Nucella lapillus* (L.): shell shape in populations from Pembrokeshire, South Wales 319

A. N. BAKER. Factors contributing towards the initiation of slug activity in the field 329

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PROCEEDINGS OF THE

Malacological Society

OF LONDON

VOLUME 40 · PART 5 · AUGUST 1973

CONTENTS

J. W. SANGER and R. B. HILL. The contractile apparatus of the radular protractor muscle of *Busycon Canaliculatum* 335

R. SEED. Absolute and allometric growth in the mussel, *Mytilus edulis* L. (Mollusca Bivalvia) 343

NIGEL F. MATHERS. Carbohydrate digestion in *Ostrea edulis* L. 359

D. S. BROWN. New species of freshwater Pulmonata from Ethiopia 369

F. H. BILGIN. Studies on the functional anatomy of *Melanopsis praemorsa* (L.) and *Zemelanopsis trifasciata* (Gray) 379

T. GASCOIGNE. A taxonomic note on the genus *Acteonia* Quatrefages 1844 395

A. BEBBINGTON and G. M. HUGHES. Locomotion in *Aplysia* (Gastropoda, Opisthobranchia) 399

BANANI CHATTERJEE and K. C. GHOSE. Seasonal variation in stored glycogen and lipid in the digestive gland and genital organs of two freshwater prosobranchs 407

R. S. K. BARNES. The intertidal lamellibranchs of Southampton Water, with particular reference to *Cerastoderma edule* and *C. glaucum* 413

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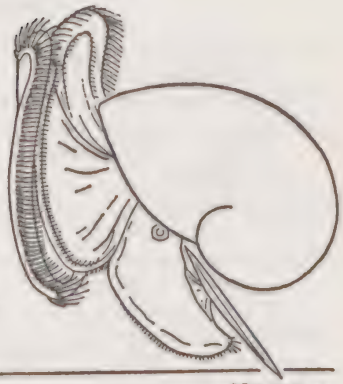

A Quarterly published by
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VOLUME 15 April 1, 1973 NUMBER 4

CONTENTS

Settlement, Growth Rates and Depth Preference of the Shipworm *Bankia setacea* (Tryon) in Monterey Bay. (3 Plates; 6 Text figures)
E. C. HADERLIE & J. C. MELLOR 265

The Genera *Chromodoris* and *Felimida* (Nudibranchia : Chromodorididae) in Tropical West America: Distributional Data, Description of a new Species, and Scanning Electron Microscopic Studies of Radulae. (3 Plates; 3 Text figures)
HANS BERTSCH, ANTONIO J. FERREIRA, WESLEY M. FARMER, & THOMAS L. HAYES. 287

Embryonic and Larval Development in the New Zealand Rock Oyster, *Crassostrea glomerata* (Gould, 1850). (3 Plates; 2 Text figures; 1 Map)
P. DINAMANI 295

Apertural Barriers in Pacific Island Land Snails of the Families Endodontidae and Charopidae. (7 Plates)
ALAN SOLEM 300

Systematics and Distribution of Western Atlantic *Ervilia* (Pelecypoda : Mesodesmatidae) with Notes on the Living *Ervilia subcancellata*. (3 Plates; 2 Text figures)
JOHN D. DAVIS 307

The Northwest American Semelidae. (2 Plates; 7 Text figures)
EUGENE V. COAN 314

Mantle Changes in the Pearl Oyster *Pinctada maxima* Induced by the Pea Crab *Pinnotheres villosulus*. (1 Plate)
TREVOR G. DIX 330

A Recent *Oreohelix* (Gastropoda : Pulmonata) from Baja California Sur, Mexico. (1 Plate; 1 Text figure)
WALTER B. MILLER 332

Notes on *Cypraea cinerea* Gmelin and *Cyphoma gibbosum* (Linnaeus) from the Caribbean Sea, and Description of their Spawn. (2 Text figures)
KLAUS BANDEL 335

[Continued on Inside Front Cover]

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

CONTENTS — *Continued*

Scanning Electron Micrographic Study of the Dorsal Integument of the Land Slug *Lehmannia poirieri* (Mabille, 1883). (2 Plates)
JOHN A. ARCADI & NORMAN HODGKIN 338
Zoogeography and Ecology of Seven Species of Panamic-Pacific Scaphopoda. (2 Plates; 3 Text figures)
M. S. MCFADIEN 340
Additional Notes on Cephalopods from Northern California.
ROBERT R. TALMADGE 348
A Note on the Anatomy of the Circumesophageal Ganglion Complex of Several Doridacean Nudibranchs. (2 Text figures)
L. DONALD PARTRIDGE, Jr. 349
Additions to the Opisthobranch Mollusk Fauna of Marin County, California, with Notes on Their Natural History. (1 Map)
TERRENCE M. GOSLINER & GARY C. WILLIAMS 352
Oxidation of C^{14}-Glucose by the Aestivating Snail *Pila globosa* (Swainson).
S. RAGHUPATHI RAMI REDDY & R. RAMAMURTHI 355
Nomenclatural Notes on West Coast *Odostomia* (Gastropoda : Pyramidellacea).
JAMES X. CORGAN 357
NOTES & NEWS 359
Status of *Obeliscus clavulus* A. Adams, 1854. JAMES X. CORGAN
Odostomia minutissima Dall & Bartsch, 1909, a Synonym of *Odostomia raymondi* Dall & Bartsch, 1909. JAMES X. CORGAN
Comments on VOKES' Paper MICHAEL D. HUBBARD (with additional comments by a referee and the editor).
Soviet Contributions to Malacology in 1971. KENNETH J. BOSS & MORRIS K. JACOBSON
BOOKS, PERIODICALS & PAMPHLETS 370

VOLUME 15 January 31, 1973 Supplement

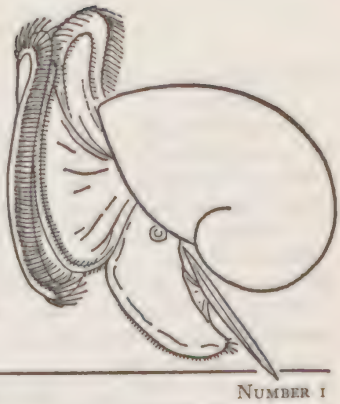
A Systematic Revision of the Recent Cypraeid Family Ovulidae

(Mollusca : Gastropoda)

BY

CRAWFORD NEILL CATE

THE VELIGER



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VOLUME 16 JULY 1, 1973 NUMBER 1

CONTENTS

The Comparative Morphology and Evolution of the Molluscan Mantle Edge. (13 Text figures)
CHARLES R. STASEK & W. ROSS MCWILLIAMS 1

A New Genus and Two New Species of Land Snails from the Lau Archipelago of Fiji (Mollusca : Pulmonata : Endodontidae) (3 Plates; 6 Text figures)
ALAN SOLEM 20

New Fossil Ashmunellas from New Mexico (Gastropoda : Pulmonata : Polygyridae). (1 Plate; 1 Text figure; 1 Table)
ARTIE L. METCALF 31

The Northwest American Psammobiidae. (4 Plates; 8 Text figures)
EUGENE V. COAN 40

A New Species of *Conus* from Indonesian Waters. (2 Plates)
WILLIAM E. OLD, Jr. 58

Reproduction, Development, and Feeding of the Australian Marine Pulmonate, *Trimusculus (Gadinia) conica*. (1 Plate; 1 Text figure)
NORINE HAVEN 61

Effect of Acetazolamide on Larval Settlement of *Ostrea lutaria*. (1 Text figure)
STEPHEN A. NIELSEN 66

The Neuroanatomy of the Osphradium in *Conus flavidus* Lamarck. (2 Plates; 1 Text figure)
C. G. ALEXANDER 68

Intraspecific Trail-Following in the Marsh Periwinkle *Littorina irrorata* Say. (1 Plate; 2 Text figures)
JOHN R. HALL 72

Estimated Growth Functions and Size-Age Relationships of the Hard Clam, *Mercenaria mercenaria*, in the York River, Virginia. (3 Text figures)
JOSEPH G. LOESCH & DEXTER S. HAVEN 76

[Continued on Inside Front Cover]

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

Second Class Postage Paid at Berkeley, California

CONTENTS — *Continued*

Some Aspects of the Biology of *Terebra dislocata* Say, 1822 (Gastropoda : Prosobranchia).
RONALD S. MOLLICK 82
An Unusual Habitat for the Rough File Shell, *Lima scabra* (Born, 1780). (1 Plate)
MORRIS K. JACOBSON & LEONARDO HERNANDEZ 85
Effect of Predation and Environmental Patchiness on the Body size of a Tropical Pulmonate Limpet. (1 Plate; 3 Text figures)
BRUCE A. MENGE 87
Maintaining Adult Bivalves for long Periods on Artificially Grown Phytoplankton.
VICTOR L. LOOSANOFF & TALBOT MURRAY, Jr. 93
Trace Metal Levels in Three Subtidal Invertebrates. (2 Text figures; 1 Map)
STANFORD R. SCHWIMER 95
A New Species of *Primovula* (Gastropoda : Ovulidae) from the Western Solomon Sea. (1 Plate)
EDWARD J. PETUCH 103
Distribution and Natural History of Opisthobranch Gastropods from Las Cruces, Baja California del Sur, Mexico. (2 Maps)
HANS BERTSCH 105
Range Extensions for Four Sacoglossan Opisthobranchs from the Coasts of California and the Gulf of California (Mollusca : Gastropoda). (2 Maps)
GARY C. WILLIAMS & TERRENCE M. GOSLINER 112
NOTES & NEWS 117
Babakina, New Name for *Babaina* Roller, 1972, Preoccupied.
RICHARD A. ROLLER
Sterkia hemphilli (Sterki) in Central California. BARRY ROTH
METHODS & TECHNIQUES 121
A Method for Marking Nudibranchs. ELIZABETH ANDERSON
BOOKS, PERIODICALS & PAMPHLETS 123

EDITOR-IN-CHIEF

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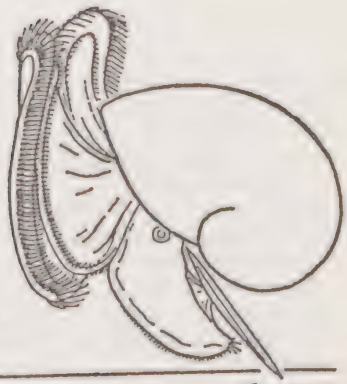

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VOLUME 16 OCTOBER 1, 1973 NUMBER 2

CONTENTS

The "Juxtaganglionic" Tissue and the Brain of the Abalone *Haliotis rufescens* Swainson. (4 Plates)
WALTER MILLER, RICHARD S. NISHIOKA & HOWARD A. BERN 125

The Northwest American Donacidae. (1 Plate; 2 Text figures)
EUGENE V. COAN 130

Techniques for Photographing Modern Mollusks. (1 Plate)
KENJI SAKOMOTO 140

A Census of Marine Prosobranch Gastropods at San Diego, California. (1 Map)
M. J. BISHOP & S. J. BISHOP 143

The Effect of Food Consumption on Growth, Fecundity, and Mortality in a Sacoglossan Opisthobranch, *Olea hansineensis*. (2 Text figures)
FU-SHIANG CHIA & MARGARET SKEEL 153

Late Pleistocene Marine Invertebrates from Rancho Miramar and Las Cruces, Southern Baja California del Sur. (1 Map)
ROBERT J. DOWLEN & JOHN A. MINCH 159

Observations on Feeding and Prey Specificity of *Tritonia festiva* (Stearns) with Comments on other Tritoniids (Mollusca : Opisthobranchia). (1 Plate)
EDGARDO D. GOMEZ 163

Fine Structure of the Eye of the Prosobranch Mollusk *Littorina scutulata*. (5 Plates)
MARGARET MAYES & COLIN O. HERMANS 166

Physiology of the Pulmonate Reproductive Tract: Location of Spermatozoa in Isolated, Self-Fertilizing Succinid Snails (with a Discussion of Pulmonate Tract Terminology). (1 Plate; 1 Text figure)
C. J. BAYNE 169

Hemochemistry and Hematology of the Aestivating Pond Snail *Pila globosa* (Gastropoda : Ampullariidae). (6 Tables)
VIJAYA BRAHMANANDAM & R. V. KRISHNAMOORTHY 176

[Continued on Inside Front Cover]

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

Second Class Postage Paid at Berkeley, California

CONTENTS — *Continued*

Morphological and Behavioral Adaptations to Desiccation in the Intertidal Limpet *Acmaea (Collisella) strigatella.* (7 Text figures)
ROGER R. SEAPY & WILLIAM J. HOPPE 181
Diversity of Feeding Mechanisms among Embryos of Pacific Northwest *Thais.* (3 Text figures)
ALANE LYONS & TOM M. SPIGHT 189
Seasonal Changes in the Body Component Indices of the Subtidal Prosobranch *Fusitriton oregonensis.* (2 Text figures)
WILLIAM B. STICKLE & JOHN P. MROŻEK 195
Type Specimens of Mollusca from the Charles R. Orcutt Collection Now at the University of California, Riverside
JACK D. MOUNT 200
Aboral Extrusion of Squid Pens by the Sea Star *Pycnopodia helianthoides.* (2 Plates; 1 Text figure)
DON R. WOBBER 203
A Review of the Marginellidae Described by BAVAY, 1903 - 1922. (8 Text figures)
BARRY ROTH & PHILLIP CLOVER 207
A New Species of Anaspidean Opisthobranch from the Gulf of California (Mollusca : Gastropoda). (1 Map; 15 Text figures)
GARY C. WILLIAMS & TERRENCE M. GOSLINER 216
Observations on the Attachment of Egg Capsules to a Substrate by *Melongena corona.* (14 Text figures)
FRASIER O. BINGHAM & HELEN D. ALBERTSON 233
NOTES & NEWS 238
Some Nomenclatural Problems in Sacoglossa. A. MYRA KEEN
The Ovulidae: Replacement Names for Four Ovulid Homonyms. CRAWFORD NEILL CATE
Subtidal Mussel Beds in Baja California with a New Record Size for *Mytilus californianus.* GORDON L. CHAN
INFORMATION DESK 243
A Source of Authors and Dates for Family Names of Gastropods. JOSEPH ROSEWATER
Differentiation: The Meaning of ICZN Article 13 (a) (i). EUGENE V. COAN
BOOKS, PERIODICALS & PAMPHLETS 246

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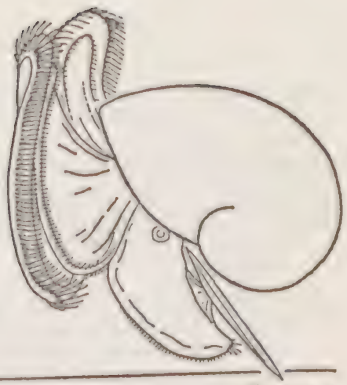

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VOLUME 16 JANUARY 1, 1974 NUMBER 3

CONTENTS

Zoogeographic Significance of a Late Quaternary Occurrence of the Bivalve *Astarte* off the Central California Coast. (1 Plate; 1 Map)
WARREN O. ADDICOTT & H. GARY GREENE 249

Some Comments on *Lobiger souverbii* Fischer, 1856, Re-Identified, of Japan (Opisthobranchia: Sacoglossa: Lobigeridae). (3 Text figures)
KIKUTARÔ BABA 253

On the Identity of *Murex triqueter* Born (Gastropoda: Muricidae). (1 Plate; 2 Text figures)
EMILY H. VOKES 258

Self-Fertilization in the Terrestrial Snail *Rumina decollata*. (1 Text figure)
ROBERT K. SELANDER, DONALD W. KAUFMAN & ROBERTA S. RALIN 265

Spawning and Development of Some Columbellidae from the Caribbean Sea of Colombia (South America). (15 Text figures)
KLAUS BANDEL 271

Some New Gastropod Representatives from the Brackish Waters of the Adriatic and Aegean Seasides. (2 Plates; 3 Text figures)
PAVLE RADOMAN 283

Observations on the Effect of Various Drugs on the Activity of the Preoral Cilia of the Prosobranch Veliger, *Conus californicus* Hinds.
ALGIRDAS G. VILKAS 289

Sabia conica (Schumacher) on the Pacific Coast of North America. (1 Plate)
I. MCTAGGART COWAN 290

Notes on Mating Behaviour of *Concholepas concholepas* (Mollusca, Gastropoda, Muricidae) from Chile.
JUAN C. CASTILLA 291

Styliola sinecosta, a New Species of Pteropod (Opisthobranchia: Thecosomata) from Barbados, West Indies. ((3 Text figures)
FRED E. WELLS, Jr. 293

[Continued on Inside Front Cover]

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

Second Class Postage Paid at Berkeley, California

CONTENTS — *Continued*

A New Subspecies of *Cyanoplax dentiens* (Polyplacophora) from San Diego, California. (1 Plate)
BARRY S. KUES 297
Estimates of Growth of *Cryptochiton stelleri* (Middendorff, 1846) in Oregon.
JOHN BEACH PALMER & PETER WOLFGANG FRANK 301
The Taxonomy and Distribution of *Marianina rosea* (Pruvot-Fol, 1930) and *Thecacera pacifica* (Bergh, 1883) comb. nov. (Opisthobranchia : Dendronotacea and Doridacea).
ROBERT BURN 305
The Ovulidae: A Key to the Genera, and other Pertinent Notes (Mollusca : Gastropoda).
CRAWFORD NEILL CATE 307
Comments on Some Pacific Coast Mollusca: Geographical, Ecological, and Chronological.
ROBERT R. TALMADGE 314
Type and Other Cephalopods in the Collection of the Department of Invertebrate Zoology, California Academy of Sciences.
ALLYN G. SMITH 319
NOTES & NEWS 334
Miscellaneous Observations on *Rumina decollata* (Linnaeus, 1758) (Achatinidae) and a Request. T. W. FISHER
Range Extension for *Dendronotus diversicolor* (Mollusca : Opisthobranchia). GORDON A. ROBILLIARD
Ethnomalacology and Archaeomolluscan Studies in North Mexico, Mesoamerica, and Central America. A Reference Bibliography. LAWRENCE H. FELDMAN
BOOKS, PERIODICALS & PAMPHLETS 341

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Malacological Review, 1974, 7: 93-100

AUTHOR INDEX FOR MALACOLOGICAL PERIODICALS

	page*
ADDICOTT, Warren O., U.S. Geological Survey, Menlo Park, California 94025, U.S.A.	91
ADEGOKE, O.S., Department of Geology, University of Ife, Ile-Ife, Nigeria	78
ALBERTSON, Helen D., Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149, U.S.A.	90
ALEXANDER, C.G., School of Biological Sciences, James Cook University of North Queensland, Townsville 4810, Queensland, Australia	87
ALLEN, J.A., Dove Marine Laboratory, Cullercoats, North Shields, Northumberland, England	78
ANDERSON, Elizabeth, Division of Entomology, University of California, Berkeley, California 94720, U.S.A.	88
ANT, H., Wielandstr. 17, D-47 Hamm, Germany	80
ARCADI, John A., Department of Biology, Whittier College, Whittier, California 90608, U.S.A.	86
ASTRE, Gaston [no address given]	71
BÁBA, Karl, Zoologischer Lehrstuhl der Pädagogischen Hochschule, Szeged, Hungary	79
BABA, Kikutarô, Shigigaoka 35, Minami-II-jyo, Sango-cho, Ikoma-gun, Nara-ken, Japan	91
BAILEY, T.G., Department of Zoology, University College of North Wales, Bangor, Caernarvonshire, U.K.	78
BAKER, A.N., Broom's Barn Experimental Station, Higham, Bury St. Edmunds, Suffolk, England	83
BANDEL, Klaus, Institut für Paläontologie der Rheinischen Friedrich-Wilhelms Universität, 53, Bonn, West Germany	85, 91
BAR, Ze'ev, Kibbutz Beth Ha'emek, Doar na Ma'aleh Hagalil, Israel	67, 68
BARBATO, G. [no address given]	73
BARBOSA, F.S., Universidade de Brasilia, Faculdade de Ciências da Saude, Brasilia D.F. 70000, Brazil	80
BARNES, R.S.K., Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, England	83, 84
BARRETT, B.W., Environmental Science Section, College of Education, Milton, Portsmouth, England	72
BARSOTTI, G., Dal Museo Provinciale di Storia Naturale, Livorno, Italy	73
BAYNE, C.J., Zoology Department, Oregon State University, Corvallis, Oregon 97331, U.S.A.	89
BEBBINGTON, A., Zoology Department, University of Bristol, Bristol, England	79, 84
BERN, Howard A., Bodega Marine Laboratory, University of California, Bodega Bay, California 94923, U.S.A.	89
BERRY, E.G., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.	79
BERRY, F.G., Nature Conservancy, 19 Belgrave Square, London SW1X 8PY, England	72
BERTSCH, Hans, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118, U.S.A.	85, 88
BESENECKER, Horst [no address given]	66
BILGIN, F.H., Zoology Department, University of Ege, Bornova-Izmir, Turkey	84
BINGHAM, Frasier O., Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149, U.S.A.	90
BISHOP, M.J., University Museum of Zoology, Cambridge CB2 3EJ, England	72, 89
BISHOP, S.J., University Museum of Zoology, Cambridge CB2 3EJ, England	72, 89
BLATCHFORD, J.G., Department of Zoology, The University, Manchester M13 9PL, U.K.	79
BOETERS, Hans D., Rumfordstr. 42, D-8 Munich 5, West Germany	79
BOLDORI, L. [no address given]	73
BORAY, J.C., Research Centre, Ciba-Geigy Ltd., Western Road, Kemps Creek, N.S.W., Australia	78
BOSCH, D.T., American Mission Hospital, Muscat, Oman	67
BOSS, Kenneth J., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.	86
BOVARD, P., Centre d'Etudes Nucléaires de Cadarache, B.P. 1, F-13 St.-Paul-lez-Durance, France	78
BRABENEC, Jaroslav, Pardubice, Czechoslovakia	66
BRAHMANANDAM, Vijaya, Department of Zoology, Bangalore University, Bangalore-1, India	89
BRANDON, Dale E., Esso Production Research Co., P.O. Box 2189, Houston, Texas 77001, U.S.A.	74

*Page numbers, this issue of *Malacological Review*.

page

BREHAUT, Roger N., La Canurie, Collings Road, St. Peter Port, Guernsey, U.K. 72
BROGGI, Jorge [no address given] 69
BROWN, D.S., Medical Research Council, c/o Experimental Taxonomy Unit, Zoology Department, British Museum (Natural History), London SW7 5BD, England 72, 83, 84
BRUGGEN, A.C. van, Department of Systematic Zoology, Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, The Netherlands 72, 80
BURCH, J.B., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A. 79, 81
BURN, Robert, Hon. Associate, National Museum of Victoria, Melbourne, Victoria, Australia 92
CAMERON, R.A.D., Department of Biological Sciences, Portsmouth Polytechnic, Hay Street, Portsmouth, England 79
CAPROTTI, Erminio, Via L.B. Alberti 12, 20149 Milano, Italy 70
CARLTON, James T., Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118, U.S.A. 82
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	page
DOWLEN, Robert J., Department of Geology, California State University, San Diego, California 92115, U.S.A.	89
DRISCOLL, E.G., Department of Geology, Wayne State University, Detroit, Michigan 48202, U.S.A.	74
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DUVAL, D.M., 49 Humberstone Road, Cambridge, England	72
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FARIA VAZ, Jorge, Alameda Lorena 1919, São Paulo, Brasil	69
FARMER, Wesley M., 1327 E. Donner Drive, Tempe, Arizona 85282, U.S.A.	85
FELDMAN, Lawrence H. [no address given]	92
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FIGUEIRAS, Alfredo, Juan Ramón Gómez 3248, Montevideo, Uruguay	69
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FISHER, T.W., Department of Entomology, Division of Biological Control, University of California, Riverside, California 92502, U.S.A.	92
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FOULQUIER, L., Centre d'Etudes Nucléaires de Cadarache, B.P. 1, F-13 St.-Paul-lez-Durance, France	78
FRANCHINI, Dario A., 37, Via Cremona, 46100 Mantova, Italy	70
FRANK, Peter Wolfgang, Department of Biology, University of Oregon, Eugene, Oregon 97403, U.S.A.	92
FRANZEN, Dorothea S., Illinois Wesleyan University, Bloomington, Illinois 61701, U.S.A.	82
FRILLI, G., Dal Museo Provinciale di Storia Naturale, Livorno, Italy	73
FULLER, Samuel L.H., Department of Limnology, Academy of Natural Sciences, Philadelphia, Pennsylvania 19103, U.S.A.	81, 82
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GASCOIGNE, T., Alleyn's School, Dulwich, London, England	84
GAUTIER, A., Laboratorium voor Paleontologie, Geologisch Institut, Rijksuniversiteit, B 9000, Gent, Belgium	72
GHISOTTI, Fernando, Via Giotto 9, I-20145, Milano, Italy	70
GHOSE, K.C., Zoology Department, Calcutta University, Calcutta-19, India	84
GITTENBERGER, E., Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands	80
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GOMEZ, Edgardo D., Scripps Institution of Oceanography, La Jolla, California 92037, U.S.A.	89
GOODHART, C.B., Department of Zoology, Cambridge University, Downing Street, Cambridge, England	79
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GREEN, J.R., Department of Computational and Statistical Science, University of Liverpool, Liverpool 3, England	72
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GROSSU, Alexandru V., Université de Bucarest, Faculté de Biologie, Spl. Independentei 93, Bucharest, Romania	66
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HADERLIE, E.C., Department of Oceanography, Naval Postgraduate School, Monterey, California 93940, U.S.A.	85
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page

Panama City Laboratory, P.O. Box 4218, Panama City, Florida 32401, U.S.A. 87
HARRIS, Stuart A., Department of Geography, The University of Calgary, 2920 24 Ave. N.W., Calgary, Alberta T2N 1N4, Canada 82
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HERNANDEZ, Leonardo [no address given] 88
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JENNER, A.B. [no address given] 71
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KADOLSKY, Dietrich [no address given] 66
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page

LAZAR, Dov, Malacological Museum, Nahariya Municipality, Israel 67
LE PENNEC, M. L. M., Laboratoire de Zoologie, Université de Bretagne Occidentale, 29 N. Brest, France 75
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MATHERS, Nigel F., Department of Zoology, University College, Galway, Ireland 84
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MONNET, R. [no address given] 71
MORANDI, V. [no address given] 70
MORE, M.T. [no address given] 71
MORE, P. [no address given] 71
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page

London NW3 7ST, U.K. 78
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POISBEAU, J. [no address given] 71
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REAL, Guy, Institut de Biologie Marine, 33-Arcachon, France 79
REDDY, S. Raghupathi Rami, Department of Zoology, University of Poona, Poona-7, Maharashtra, India 86
REX, Michael A., Department of Biology, University of Massachusetts-Boston, Boston, Massachusetts 02116, U.S.A. 79
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ROBERTSON, Robert, Academy of Natural Sciences, Nineteenth and Parkway,

page

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RUFF, Michael D., Department of Zoology, Rice University, Houston, Texas 77001, U.S.A. 81
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SANGER, J.W., Department of Anatomy, University of Pennsylvania, School of Medicine, Philadelphia, Pennsylvania 19104, U.S.A. 84
SCHELTEMA, A.H., Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, U.S.A. 79
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SEAPY, Roger R., Department of Population and Environmental Biology, University of California, Irvine, California 92664, U.S.A. 90
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SELANDER, Robert K., Department of Zoology, University of Texas, Austin, Texas 78712, U.S.A. 91
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STARMÜHLNER, F., I. Zoologischen Institut der Universität Wien, Wien, Austria 79
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STILES, S.S., U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Milford, Connecticut 06460, U.S.A. 81
SZIGETHY, Anna [no address given] 66
TALMADGE, Robert R., Field Associate, Department of Invertebrate Zoology, California

	page
Academy of Sciences, San Francisco, California 94118, U.S.A.	86, 92
TARDY, J., Laboratoire de Biologie et Biochimie Marines, IUT de la Rochelle, B.P. 536, rue de Roux, 17000 La Rochelle, France	78
TAUNAY, F. [no address given]	71
TESIO, Călin, Université de Bucarest, Faculté de Biologie, Spl. Independentei 93, Bucarest, Romania	66
TESKEY, Margaret C., P.O. Box 273, Big Pine Key, Florida 33043, U.S.A.	82
THOMAS, Ronald F., Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149, U.S.A.	82, 83
THOMPSON, T.E., Zoology Department, University of Bristol, Bristol, England	72, 79, 83
TIMMERMANS, L.P.M., Zoological Laboratory, Agricultural University, Wageningen, The Netherlands	78
TOFFOLETTO, F., Via Marcona 26, 20129 Milano, Italy	73
TRUEMAN, E.R., Department of Zoology, The University, Manchester M13 9PL, U.K.	79
UETA, Marlene T., Instituto de Biologia, Universidade Estadual de Campinas, 13100 Campinas, São Paulo, Brazil	82
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VOKES, Emily H., Department of Zoology, Tulane University, New Orleans, Louisiana 70118, U.S.A.	91
VOVELLE, Jean, Histologie et cytologie des Invertébrés marins, Université de Paris, Paris VI, France	78
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WOBBER, Don R., Department of Marine Biology, California State University, San Francisco, California 94122, U.S.A.	90
WOLDA, H., Smithsonian Tropical Research Institute, Balboa, Canal Zone	67
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YARON, I., Rehov Hagalil 51, Haifa, Israel	67, 68
YOUNG, Richard Edward, Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822, U.S.A.	82
YOUSIF, Fouad, Laboratory of Bilharziasis Research, National Research Centre, Cairo, Egypt	74, 75
ZILCH, A., Senckenberg Museum, Senckenberg-Anlage 25, D-6 Frankfurt/M. 1, Germany	66

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7

ON THE COVER - Keyhole limpets. Illustrations by John L. Tottenham.

1974

MALACOLOGICAL REVIEW

7

1974

CONTENTS

Research Articles

Reproductive behavior and early development in *Littorina scabra angulifera* and *Littorina irrorata* (Gastropoda: Prosobranchia) in the Tampa Bay region of Florida. S. B. GALLAGHER and G. K. REID 105

Relationships of Eurasian-North African *Ancylus* to the North American *Rhodacmea* (Pulmonata: Ancylidae) as shown by apical shell sculpture. J. B. BURCH 127

Brief Communications

Notes on the spawning and hatching of three species of marine gastropods. R. KASINATHAN, K. GOVIDAN and R. NATARAJAN 133

Necrophagous habit in *Opeas gracile* (Stylommatophora: Subulinidae). T. R. MITRA and S. K. BISWAS. 136

Miscellanea

Titles in *Occasional Papers on Mollusks* 137

News and Announcements

Symposium on Littorinidae 162

Change in editorial and business offices of *Malacologia* 162

Société Française de Malacologie 162

Book Reviews

Polyplacophora of the Caribbean region, reviewed by R. C. BULLOCK. 163

Flukes and Snails, reviewed by H. D. BLANKESPOOR 165

Malacological Calendar 166

Contents of Current Malacological Periodicals 167

Author index for malacological periodicals. 192

Publications. 196

Index 202

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Vol. 2: *Stagnicola* (Lymnaeidae)
Vol. 3: Epitoniidae (wentletraps)
Vol. 4: Conidae (cone shells)
Vol. 5: *Dysnomia* (freshwater mussels)
Vol. 6: Freshwater gastropods of the Lake Ohrid region, Yugoslavia
Vol. 7: Keyhole limpets

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Malacological Review, 1974, 7: 105-125

REPRODUCTIVE BEHAVIOR AND EARLY DEVELOPMENT IN *LITTORINA SCABRA ANGULIFERA* AND *LITTORINA IRRORATA* (GASTROPODA: PROSOBRANCHIA) IN THE TAMPA BAY REGION OF FLORIDA

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ABSTRACT

Reproduction in ***Littorina scabra angulifera*** (Lamarck) and ***Littorina irrorata*** Say was studied in the Tampa Bay, Florida, area. In both species copulation and spawning were correlated with lunar phases and daily tidal rhythm. Reproductive activity in *L. s.* ***angulifera*** was seasonal, there being little or none from November to May. In *L.* ***irrorata*** reproductive activity was sporadic and spawning was greatest during spring and summer. Copulation in *L.* ***irrorata*** occurred in most months but was rare in winter. One spawning was noted in January.

It was found that water must be present for release of spawn by ***Littorina scabra angulifera***; deprivation of access to water disrupted spawning and caused a loss of viable spawn. Mortality due to water deprivation was higher among gravid females than among males and non-gravid females of *L. s.* ***angulifera***. Subjecting snails of both species to the constant environment of laboratory experimental tanks disrupted but did not stop reproductive activity.

Comparative studies of individuals of both species from marsh grass (***Spartina***) habitats with those from seawalls revealed that snails attained greater size in the former community. ***Littorina scabra angulifera*** females released a greater amount of spawn and over a longer period of time in the marsh grass habitats than on seawalls.

Development from fertilized egg to the swimming veliger stage was similar in both species but, at 26-28°C, took only 27-40 hours in ***Littorina irrorata*** as compared to 4 days in *L.* ***scabra angulifera***.

INTRODUCTION

Littorina scabra angulifera (Lamarck) and *L. irrorata* (Say) are supratidal snails that occur abundantly in the Tampa Bay, Florida, area. Both species live in quiet-water communities of marsh grass (*Spartina* sp.), red mangrove (*Rhizophora mangle*) and on man-made structures such as pilings and seawalls, usually above the waterline. *L. s. angulifera* is a tropical species ranging southward from Cedar Key, Florida, on the Gulf coast and St. Augustine on Florida's Atlantic coast through the Caribbean to the coast of Brazil. It has been reported in Bermuda, is known to inhabit the western coast of Africa and has migrated through the Panama Canal (Bequaert, 1943). *L. irrorata* is a snail of the temperate region of the Atlantic and Gulf coasts of the United States, i.e., from Indian River, Florida, to Long Island Sound, New York, and from Charlotte Harbor, Florida, to the Rio Grande River, Texas (Bequaert, 1943).

Rosewater (1963) has proposed that the species previously designated *Littorina*

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angulifera is a subspecies of *L. scabra*. Thus, reference in this paper will be to *L. s. angulifera* and, where appropriate, to *L. s. scabra*.

Mating behavior and copulation have been studied in various species of *Littorina*. Linke (1934) and Fretter & Graham (1962) described copulation in *L. littorea*. Gibson (1964) studied mating behavior and copulation in detail in *L. planaxis*. Lenderking (1954), in studying the biology of *L. scabra angulifera* in the Miami area, found that copulating pairs of this species were more numerous following the quarter moon than at other lunar phases and that rainfall apparently caused an increase in mating activity. Struhsaker (1966), in a study of 3 Hawaiian littorinids (*L. picta*, *L. pintado* and *L. s. scabra*), noted that *L. s. scabra* frequently formed male to male pairs and that it also paired, though infrequently, with *L. pintado*. This type of behavior had been previously reported for northern *Littorina* by Linke (1934). Apart from the above studies, we have scant information on mating and copulation in littorinids.

Spawning in littorinids, on the other hand, has been studied more extensively. Early work by Tattersal (1920), Hayes (1929) and Linke (1934) dealt with northern species. The ecology and reproduction of 4 British littorinids have been discussed by Fretter & Graham (1962). Rosewater (1970) classified the littorinids according to type of spawn released. Most species release pelagic eggs in capsules, but a few species, such as *Littorina obtusata*, *L. atakana* and *L. sitkana*, lay egg masses. Others, such as *L. scabra angulifera*, *L. s. scabra* and *L. saxatilis*, are ovoviviparous. Of this last group, the first 2 retain young in the mantle cavity until the swimming veliger stage develops, whereupon they are released into the water. *L. saxatilis* retains young in the mantle cavity until the crawling snail stage (Rosewater, 1970). Studies of spawning behavior in littorinids reveal that, in many species, spawn release is related to the lunar or daily tidal cycle (Fretter & Graham, 1962; Lenderking, 1954; Struhsaker, 1966; Borkowski, 1970; Marcus & Marcus, 1963).

Lebour (1945) reported that spawning in *Littorina scabra angulifera* in Bermuda occurred only during July and August. At that time she noted that the snails remained near the waterline. Lenderking (1954), studying the biology of *L. s. angulifera* in the Miami region, found that spawning continued through the year. She also described copulation, spawn release and a bi-lunar spawning periodicity in this snail. Marcus & Marcus (1963) studied the reproductive anatomy of several littorinids on the coast of Brazil, among them *L. s. angulifera*. Bingham (1972a) reported that reproductive activity of *L. irrorata* in a marsh in North Florida occurred from May to September. He described the anatomy of the penis, the process of copulation and that of spawn release in the form of encapsulated eggs.

The present paper is part of a study on the life history of both *Littorina scabra angulifera* and *L. irrorata* in the Tampa Bay, Florida, area and is concerned with the factors affecting mating and spawning of these snails together with observations on copulatory and spawning behavior. It was undertaken because preliminary work revealed differences in reproductive behavior of *L. s. angulifera* located in the Tampa area as compared with those in the Miami area studied by Lenderking (1954). It was thought that the local study would further our knowledge of the effects of the external environment upon the behavior and life history of these species. Also, it was felt that a comparison of the reproductive process in 2 closely related species in the same habitat would be informative.

THE HABITATS

The animals used in this study inhabited 2 distinctively different habitats. One consisted of natural marsh grass-mangrove communities which occur commonly

throughout the Tampa Bay area. Animals from 2 such areas were observed. Both were on Mullet Key (Ft. DeSoto Park), which is located at the mouth of Tampa Bay (27°37' N. lat., 82°44' W. long.). One of these areas is a small strand (50 m in length) on Mullet Key Bayou which contained numerous small red mangrove trees (*Rhizophora mangle*) in addition to the marsh grass *Spartina* sp. The substrate here was sandy mud, portions of which were quite soft. The second natural area was a small *Spartina* marsh at the north end of Mullet Key landward of a sand beach on the Gulf of Mexico. The substrate here was sand and there were no young mangrove trees other than very small seedlings. The second habitat was a seawall bordering a canal located in Boca Ciega Bay immediately south of John's Pass in Treasure Island. The substrate at the base of the seawall was soft mud and clay or oyster reef. The lower 20-40 cm of the wall were encrusted with growths of oysters (*Crassostrea virginica*) and barnacles (*Balanus amphitrite* and *Chthamalus* sp.). The seawall rises 120-140 cm above the bottom of the canal and is constructed of concrete slabs 120 cm wide. These slabs were used as quadrats in all studies involving population counts and random samples of snails. Because of the ease of studying animals in this habitat, the most detailed quantitative information was obtained here. Nevertheless, animals from natural habitats, such as *Spartina*, were studied in order to compare them with seawall populations. The salinity of the seawater in all areas ranged from 34-35‰. Shallow water temperatures were similar in both habitats and varied from highs of 30-32°C during July and August to lows of 16-20°C during January and February. These shallow water temperatures were more variable than Gulf water temperatures.

METHODS

All observations on mating behavior and copulation were made on animals from the seawall colony during the period of June, 1971, to September, 1971. Spawning was studied from June, 1971, through September, 1972, and included animals from *Spartina*-mangrove habitats as well as those on the seawall. In addition, both mating behavior and spawning were studied in animals placed in aquaria in the laboratory.

The percentage of ***Littorina scabra angulifera*** pairing at different phases of the lunar and daily tidal cycle was determined by counting the number of pairing snails in 11 seawall quadrats after first determining the total *L. s. angulifera* population for this area. Although *L. irrorata* were present in the same location, the population density was not sufficient to obtain significant quantitative data regarding percentage of pairing at lunar and daily tidal phases.

The process of pairing and copulation was studied, in both species, with animals in aquaria. The sex of the snails could be determined in the living animal by the presence or absence of a penis which, in the male, is located ventroposteriorly to the right tentacle. A study of the gross reproductive anatomy was done on animals that had been relaxed in cold seawater containing 5-10% ethyl alcohol. After removal from the shell such animals remained relaxed and could be studied easily. They could then be preserved if desired by placing them directly in a fixative.

Among ***Littorina scabra angulifera,*** the percentage of gravid females was determined on successive days of the breeding cycle by noting the presence of spawn in the mantle cavity of the living animal (Lenderking, 1954). The spawn, which consists of eggs or embryos, appears as a cream-colored or yellow mass in the roof of the posterior portion of the mantle cavity. Although it can be seen with the naked eye, the use of a 10-power dissecting microscope enabled very thin spawns to be detected. In this way the percentage of gravid females at any given time could be determined without depleting the population. Since *L. irrorata* does not deposit spawn in the mantle cavity, but releases egg capsules, spawning in this species was studied by observing isolated females.

In order to study spawn release in both species, ripe females, collected 1-2 days before

full or new moon dates, were isolated in small aquaria. These were glass or plastic bowls approximately 9 cm in diameter containing seawater (salinity 34-35‰) 2-3 cm deep and kept at a room temperature of 26-28°C. The time of day that the isolated females released spawn was recorded to determine if there were daily rhythms. Individuals of both species were observed for pairing and spawning activity throughout the year to ascertain if reproductive activity was continuous and if peak periods of such activity occurred.

Groups of animals of both species were also kept under the relatively constant conditions of an aquarium in order to determine if reproductive activity could occur under those circumstances. Experiments involving the effects of water deprivation on spawning in *Littorina scabra angulifera* were also undertaken.

Littorina scabra angulifera that spawned in the aquaria were usually returned later to their original habitat. In order to follow their subsequent behavior, several groups were marked with waterproof paint. It was noted that they resumed positions on the seawall and eventually spawned normally.

The number of larvae or eggs released during spawning in both species were estimated by counting the number of veligers or eggs (preserved in formalin) in a dish placed over a grid pattern. Twelve to 16 random grids in the pattern were counted and the total number of larvae or eggs released estimated therefrom. Although this method gives only a general estimate, the numbers spawned were quite large and it was therefore felt that sufficient information was obtained. Development from the fertilized egg to the swimming veliger was observed and described briefly for both species. No studies were made of development from the swimming veliger to metamorphosed snails.

OBSERVATIONS AND RESULTS

Mating Behavior: *Littorina scabra angulifera* and *L. irrorata*

Periodicity

Mating behavior of *Littorina scabra angulifera* in the Tampa Bay area followed a bi-lunar periodicity, a daily tidal periodicity and seasonal variation. Table 1 shows the numbers and percentages of snails pairing on different days of 4 separate breeding periods. The data show that pairing reached a maximum between the quarter moon and the full or new moon. By the full or new moon, the number of snails mating had diminished to an occasional pair.

Table 2 shows the relationships of pairing to daily tidal rhythm in 2 mating periods before the full moon. The data indicate that the percent of mating pairs varied with the daily tidal cycle. Pairing was greater during high tide periods than during low tides. Rainfall during a low tide period, however, was correlated with a rise in pairing frequency (see data for 1 and 2 August, Table 2). It was noted that rainfall during other phases of the lunar cycle was not followed by increased pairing.

Observations on pairing in *Littorina irrorata* were made also. Although this species did not occur in sufficient numbers on the seawall to obtain any quantitative data, observations indicated that pairing in this snail follows a bi-lunar periodicity too. In *L. irrorata* pairing occurred near and during full and new moon times. The dates of maximum pairing in the 2 species overlap, so that pairs of both species can be found at the same time. Only very rarely can pairs of either species be found after the full or new moon and before the quarter moon. Pairs of *L. scabra angulifera* were distributed randomly on the seawall and not confined to any specific level of it, but pairs involving *L. irrorata* were almost always near the water level.

Copulatory Behavior

Observations on pairs of both species revealed that occasional male to male pairs were formed. Female to female pairs were never found. In one group of *Littorina*

TABLE 1. Lunar periodicity of mating in *Littorina scabra angulifera*. The number of snails represents the largest number pairing on the date shown. Total snail population was counted every 2 weeks; percentages are based on this number.

Date 1971	Total pop.	No. of individual snails pairing	% snails pairing	Moon phase
1 June	766	–	–	first quarter
2 June		2	<0.5	
3 June		6	<0.5	
4 June		80	10.4	
5 June		70	9.1	
6 June		44	5.8	
7 June		16	2.1	
8 June		6	<0.5	
9 June		4	<0.5	full moon
10-12 June	no pairs found			
15 June	786	2	<0.5	
16 June		–	–	last quarter
17 June		40	5.1	
18 June		92	11.6	
19 June		92	11.6	
20 June		–	–	
21 June		–	–	
22 June		4	<0.5	new moon
30 June	790	–	–	first quarter
1 July		–	–	
2 July		70	8.8	
3 July		122	15.4	
4 July		174	22.0	
5 July		134	17.0	
6 July		22	2.8	
7 July		14	1.8	
8 July		–	–	full moon
30 July	564	–	–	first quarter
31 July		54	9.2	
1 Aug.		56	10.0	
2 Aug.		164	29.2	
3 Aug.		142	21.2	
4 Aug.		20	3.5	
5 Aug.		–	–	
6 Aug.		occasional pair	<0.5	full moon
7-9 Aug.	no pairs found			

scabra angulifera, mixed and separate sexes were studied in aquaria to determine the prevalence of such intra-sex pairing. There were 3 aquaria of 40 snails each. One contained 20 males and 20 females; a second, 40 males; and the third, 40 females. All were freshly collected animals. At the end of 1 hour there were 5 copulating male to female pairs in the first aquarium. There were 3 pairs in the second group containing 40 males, one of which was attempting to copulate. There

TABLE 2. Daily tidal rhythm of mating in *Littorina scabra angulifera* in 2 mating periods before full moon. Tide is expressed in terms of height of water on the seawall in cm at any given time. A water level of "0" indicates that the water was below the base of the seawall and includes low water of neap tides as well as mean low water and extreme low water of spring tides. Since this snail was almost never found below the encrusted base of the seawall, it was not thought necessary to include specific data on tides lower than this demarcation.

Date	Time	Water level (in cm)	Pairing snails	% pairing snails	Total pop.
4 June	0930	41	80	10.4	766
	1130	32	62	8.1	
	1315	13	8	1.1	
	1515	0	0	0.0	
	2030	10	32	4.2	
5 June	0630	18	34	4.4	766
	0915	35	70	9.2	
	1000	43	62	8.1	
	1130	36	50	6.5	
	1400	6	10	1.3	
	1600	0	0	0.0	
6 June	0730	35	44	5.7	766
	0945	48	38	4.9	
	1130	48	36	4.7	
	1730	0	0	0.0	
	2145	0	4	0.5	
1 Aug.	0830	40	56	10.0	564
	1000	30	40	7.1	
	1500	0	0	0.0	
	*1900	4	66	11.7	
	2400	28	96	17.0	
2 Aug.	0830	51	164	29.2	564
	1130	26	144	25.5	
	1545	0	14	2.5	
	**1930	0	96	17.0	
	2400	23	72	12.7	
3 Aug.	0900	58	142	25.2	564
	1200	48	96	17.0	
	1530	-	-	-	
	1930	0	2	0.4	
	2230	16	26	4.6	
4 Aug.	0900	58	20	3.5	564
	1330	34	20	3.5	
	1600	0	4	0.7	
	1930	0	0	0.0	

* Rain at approximately 1900 hours

** Rain at approximately 1730 hours

were no pairs in the third group of 40 females. Apparently it is the males that seek partners, as females did not assume the position of the male. The mechanism by which this is accomplished is not known, but during experiments in directional motion snails were seen to follow the trails of other snails and tended to move in lines of from 2 to 5 individuals rather than singly.

Mating or attempted mating between the 2 species was also observed. Examination of such pairs revealed that in many instances 2 males were involved or that actual copulation did not take place. The number of mixed pairs varied with the relative numbers of the 2 species. In one area of seawall containing 399 *Littorina scabra angulifera* to 262 *L. irrorata*, there was a total of 29 *L. s. angulifera* pairs, 5 *L. irrorata* pairs and 6 mixed pairs. In still another area, observed at the same time, containing only 100 *L. irrorata* to over 700 *L. s. angulifera*, there were 87 pairs of *L. s. angulifera*, no pairs of *L. irrorata* and 3 mixed pairs. Apparently, contact with a *Littorina* shell by the male during the mating phase of the breeding cycle may induce mating behavior.

During pairing in both species, the male firmly attaches with the foot to the right side of the female. The female meanwhile is firmly attached to the substrate with her foot. Such pairs may or may not be copulating. To observe the copulation process, the female of the pair is allowed to crawl on a finger or an object that can be held, while the shell is tipped to give a view of the mantle cavity. If the male is not disturbed, this maneuver will not disrupt the mating process. During copulation the entire penis is placed in the mantle cavity of the female over the right side of the aperture of the shell. The basal portion of the penis is much enlarged and is pressed against the roof of the mantle cavity. Only the thin distal portion is inserted into the opening of the oviduct, which can be seen as a white protuberance on the floor of the mantle cavity of the female. Apparently, the enlarged basal portion of the penis serves to hold the thin portion in place during release of sperm. In many species of *Littorina* the basal portion of the penis contains mucus secreting glands which help hold it in place during copulation (Fretter & Graham, 1962; Gibson, 1964; Struhsaker, 1966; Marcus & Marcus, 1963), but none were visible grossly in either *L. scabra angulifera* or *L. irrorata*.

Copulation in either species lasted no more than 1 hour, usually between 20-40 minutes. In *Littorina scabra angulifera* occasional pairs may remain together for several hours after actual copulation has been completed. The animals were completely withdrawn into their respective shells and were attached to the substrate and to each other only by dried mucus. *L. irrorata* did not remain paired after copulation.

Pairing in *Littorina scabra angulifera* was not observed in the field from November, 1971, through mid-April, 1972, but occasional pairs formed when groups of animals were placed in aquaria during these months. At this season there was little or no spawning. *L. irrorata* was seen to pair occasionally in the field during November-April, but no spawning was detected except during the January new moon period. *L. s. angulifera* kept in aquaria tended to pair at any time in the lunar cycle and without regard to tidal periodicity. In 2 groups of *L. s. angulifera* kept in aquaria for 2 weeks (1 complete breeding period), mating was seen to occur continuously for 11 days in one and 8 days in the other, considerably longer than the usual 4-5 day peak observed in the natural habitat. In *L. irrorata* kept in aquaria for 2 week periods, mating was found to occur at any time of day or night but did not extend over prolonged periods.

Reproductive Systems, Size at Sexual Maturity

The anatomy of the male and female reproductive systems of *Littorina scabra*

angulifera from Brazil was studied in detail by Marcus & Marcus (1963). Our observations concur generally with theirs. In addition, however, it was found in the male that, during the mating period, the testicular duct is prominent and full of sperm. The gonad itself is located in the visceral coil, intertwined with the digestive gland. The reproductive anatomy of *L. irrorata* is similar, the major difference being that the prostate gland is bright vermillion instead of white as in *L. s. angulifera*. The anatomy of the penis is slightly different (Morrison, pers. comm., 1972; Bingham, 1972b). In this species, the organ consists of a swollen basal portion and a thinner distal portion, but the basal portion is less distinct and there is no brown bean-shaped appendage as seen in *L. s. angulifera*.

In female *Littorina scabra angulifera*, the oviduct occupies a position next to the rectum on the right side of the mantle cavity. It is white and leads to a white covering gland. Since no capsule is produced in this species, no capsule gland is present. When dissected after copulation but prior to spawning, the gonad can be seen as a branched yellow gland in the viscera dorsal to, and intertwined with, the digestive gland. The oviduct is swollen and filled with sperm. After spawning, all female organs are reduced in size. As in the male, the general reproductive anatomy of female *L. irrorata* is similar to that in *L. s. angulifera*. The oviduct occupies the same relative position, but it is buff-colored and leads to a large pinkish-buff and white capsule and covering gland. This structure is much larger and more complex than its homologue in *L. s. angulifera* since eggs are enclosed in a capsule and glands for secreting it must be present. The ovary is greenish rather than yellow.

The sex of *Littorina scabra angulifera* could not be determined in animals smaller than approximately 5.0 mm shell height as neither penis nor oviduct were visible grossly. At approximately 5.0 mm shell height, however, a small translucent crescent-shaped penis could be seen. At shell heights of 7-8 mm, the penis had differentiated into the basal and distal portions. By 9.0 mm shell height, the penis had its adult appearance. Females less than 7.0 mm shell height had no grossly visible oviduct or covering gland, but at approximately 7.5 mm shell height, the oviduct and covering gland are apparent. The smallest females found producing spawn had a shell height of 8.7 and 8.9 mm, respectively, but spawning in females below 13.0 mm was rare. Since small sizes of *L. irrorata* were not generally available, no study of the development of reproductive structures was done on this species. Bingham (1972b), however, noted that sex could be determined in animals of 6 mm or more. The reproductive anatomy of both of these species is similar to that described for *L. littorea* by Fretter & Graham (1962).

Size differences in sex and habitat

Measurement of the total shell height of *Littorina scabra angulifera* from seawall and *Spartina* habitats showed that there were size differences between the 2 groups as well as between sexes. Among a total of 467 *L. s. angulifera* from the seawall, the mean shell height of males was 13.84 mm and of females 14.98 mm. Among a sample of 170 *Spartina* marsh snails, the mean shell height of males was 20.20 mm and of females 22.40 mm. The difference in size between the sexes was found to be significant (F test, $p = 0.01$). The size of spawning females in both seawall and marsh grass snails reflects the size difference shown by the 2 groups. Among seawall animals nearly 70% of spawning females were from 13.0 to 17.0 mm in shell height, but among the marsh grass animals the greater proportion of spawning females were between 20.0 and 25.0 mm in shell height.

Measurements of 432 *Littorina irrorata* from marsh grass habitats showed that there was no significant difference in the mean shell height of males and females (21.01 mm for males, 21.22 mm for females). However, among animals greater

than 24.0 mm shell height (39 individuals in this sample) nearly 70% (27 individuals) were female. Bingham (1972a) reported similar data for *L. irrorata* in a marsh in North Florida. As in *L. scabra angulifera*, the mean shell height of *L. irrorata* from the seawall was less than that of *Spartina* marsh animals, it being 10.07 mm.

Spawning: *Littorina scabra angulifera*

Bi-lunar periodicity in spawning

Spawning by *Littorina scabra angulifera* in the Tampa Bay area has a bi-lunar periodicity, a daily tidal rhythm, and seasonal variation as observed in mating behavior. Figure 1, which covers observations made from August, 1971, through November, 1971, shows that spawning began at the time of full and new moon, as evidenced by the increase in the percentage of gravid females up to the dates of full or new moon and the subsequent decline in the percent of such females after these dates. Spawning in gravid females placed in isolated aquaria 1-2 days before full or new moon dates was also found to start at the date of full or new moon and to continue for approximately 4-5 days thereafter. Different females spawned on different days. No female *L. s. angulifera* studied ever spawned on more than 1 day of 1 breeding period.

Figure 2 shows that in the Tampa Bay area peak spawning occurred during July, August, September and early October. Spawning was not detected in seawall animals from the end of November until the end of April; it declined sharply after mid-October. Only occasional females in this location spawned during late October and early November and again at the very end of April and during all of May. It was not until June that 10% or more of the females spawned. Spawning in snails from the marsh grass habitat did not decline sharply until the end of November. Thereafter, occasional spawning females were found during some of the winter months, but resumption of regularly detectable spawning in the spring occurred at the end of April as in the seawall colony.

Frequency of spawning

Studies of marked females that had spawned in aquaria and were subsequently returned to the seawall indicated that individual snails spawned in alternate breeding periods or even further apart. Only 1 of these females was found to spawn in 2 successive periods. This, however, may be due to adverse effects of isolation in small aquaria without food for 5 or 6 days or to the low percentage of marked animals recovered after this procedure. Data in Fig. 2 show that on the seawall some females must spawn in successive breeding periods since the combined percentages for any 2 successive periods in the peak breeding season add up to more than 100%. Spawning in 2 successive periods also occurred in many individuals in groups of animals kept in aquaria and fed for 2 week periods. Such groups were collected prior to spawning; the gravid females were isolated and allowed to spawn in aquaria and then returned to the group.

It is evident from Fig. 2 that spawning in *Littorina scabra angulifera* is confined to the warmer months (June to November) in the Tampa Bay area. No direct correlation between rainfall and spawning was noted as high percentages of spawning occurred during dry periods as well as wet. Rather, spawning seemed to be correlated directly with lunar periodicity in that gravid females were found near the new and full moon dates but not at the quarter moon dates. The season of peak breeding activity did correspond with the rainy season, however.

Spawn deposition and release

In *Littorina scabra angulifera*, spawn is deposited in the mantle cavity and held

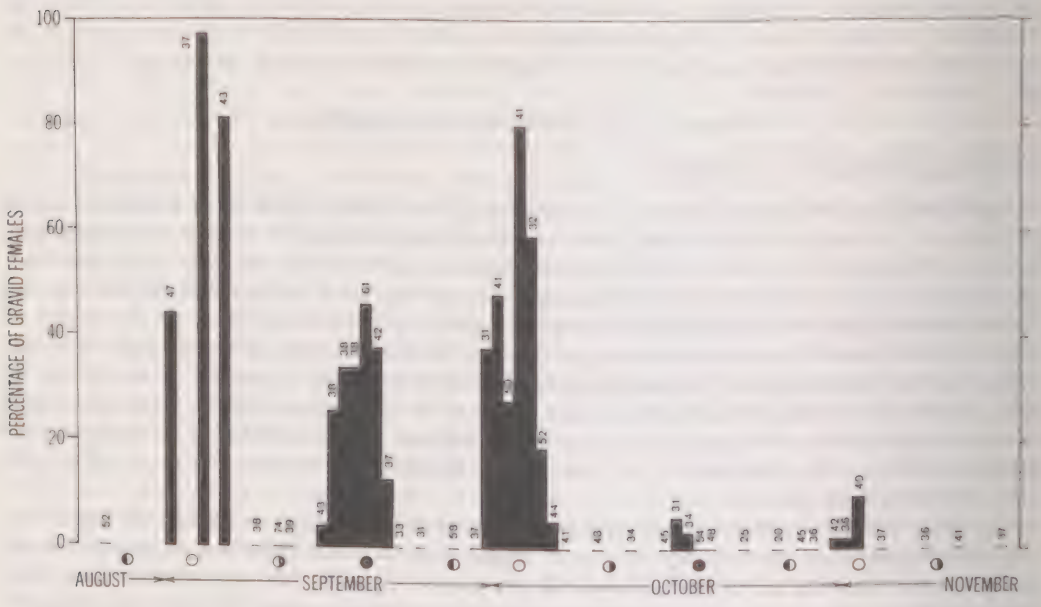

FIG. 1. Bi-lunar periodicity in the occurrence of gravid female *Littorina scabra angulifera*, August to November. Moon phases are shown on the horizontal axis. Figures at the end of each histogram denote sample size.

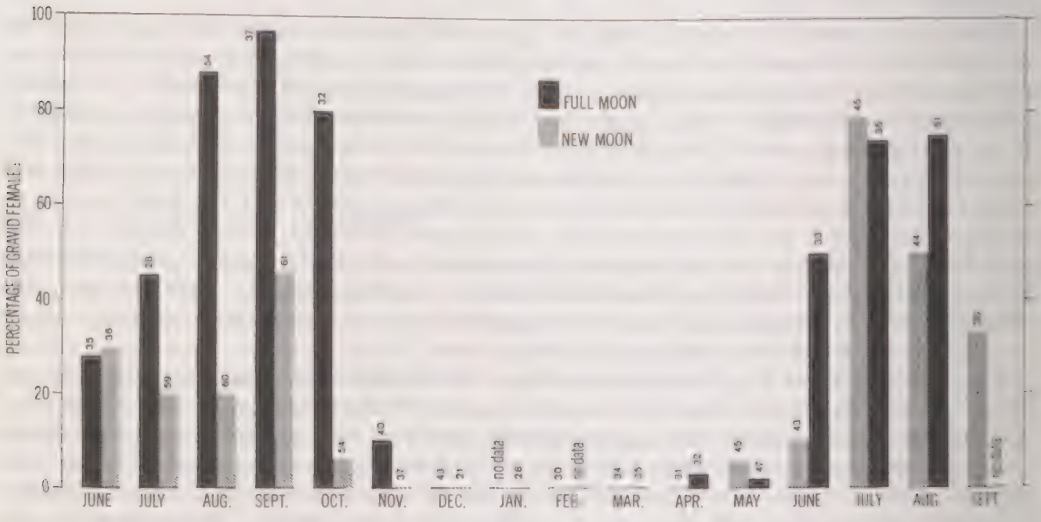

FIG. 2. Seasonal occurrence of gravid female *Littorina scabra angulifera*, June 1, 1971, to mid-September, 1972. Figures at the end of each histogram represent sample size.

in place in rows between gill leaflets by thick mucus (see also Lenderking, 1954; Marcus & Marcus, 1963). When removed from the mantle cavity, the egg mass will come free as a sheet with the eggs in rows adhering to one another. It was found that eggs were in the 1-celled stage prior to release of polar bodies when first deposited. In some cases, the eggs thus removed developed normally and in others many abnormal cleavages occurred with development rarely going beyond the trochophore stage. Normally, spawn remains in the mantle cavity until it reaches the swimming veliger stage when it is released into the surrounding water. Examination of females during spawn release showed that hatching usually occurred in the mantle cavity. It took 4 days from fertilized egg to hatched veliger at room temperatures of 26-28°C. Judged from the lapse in time between mating and spawning, this is probably the length of time development takes in the field also. No outer capsule is produced in *L. s. angulifera*; the embryos are encased in an egg covering only. The size of the egg with its covering ranged from 0.085 to 0.099 mm in diameter. The size of the egg itself was uniformly 0.071 mm in diameter. These sizes were slightly larger than those reported by Lenderking (1954) and slightly smaller than those reported by Lebour (1945). The size of the veliger shell at hatching was from 0.114 to 0.128 mm in length.

Actual spawn release was first observed in females in isolated bowls. To spawn, the female travelled to the bottom of the bowl and crawled, submerged, for as long as 1 hour or as little as 5-10 minutes before spawning. In some instances the female crawled vertically out of the water to spawn at a later date. Animals in the bowls always spawned when either partially or completely submerged, although at other times they usually remained out of the water at the top of the container. There appeared to be no consistent orientation of the body of the female during spawning, but the aperture was always covered with water. On the seawall, spawning females did not actually submerge but spawned in the wash zone within about 6 cm of the water line so that they were intermittently covered by water as waves lapped at the wall. The snails were almost always head down as they must migrate down the wall (head first) in order to reach the wash zone.

All spawn was released at one time in a series of spurts, the process taking as little as 2 minutes in smaller seawall animals or up to 20-30 minutes in larger marsh grass animals. The spawn could be seen as a yellowish cloud emerging from the right side of the shell aperture. To accomplish this release, the animal tipped the shell up and appeared to take in a stream of water; the edge of the shell was then depressed as the larvae streamed out. The animal also put snout and tentacles into the mantle cavity as if attempting to push the spawn out. This process was the same on the seawall and in the aquaria. When spawning was completed the female moved to the top of the bowl, or if on the seawall, to a higher, drier level. Examination of animals immediately after spawning revealed that all the spawn had been released since none remained in the mantle cavity.

That the female can store sperm was shown by studying a group of females that were isolated from males for part of the mating period. On the date of isolation, 45% of 47 females contained spawn. Subsequent examination of these animals revealed that after 6 days isolation 83% contained spawn. After this time spawn release began and no new individuals produced eggs.

Daily tidal periodicity in spawning

The present study shows that there is also a daily tidal rhythm in spawning in *Littorina scabra angulifera*. The time of spawning in 139 females examined from the 23-27 June to the 6-10 August breeding periods was found to correlate with

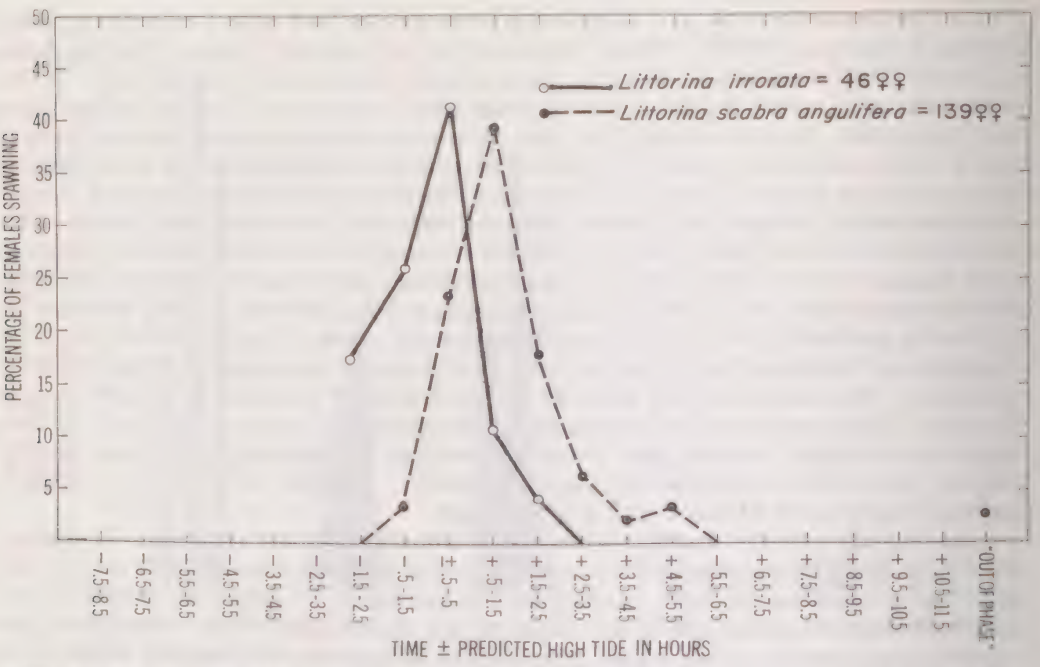

FIG. 3. Spawning in *Littorina irrorata* and *L. scabra angulifera* as related to high tide during the breeding season.

the highest tide for the date. Figure 3 shows that approximately 63.3% of these animals released spawn from 30 minutes before to 1.5 hours after the highest tide for the date. Approximately 24.5% released spawn between 1.5 and 3.5 hours after the highest tide, 5.8% spawned from 3.5 to 5.5 hours after predicted high tide, and 2.9% released spawn near midnight, which would be approximately 12 hours "out of phase." Only 3.6% released spawn between 1.5 and 0.5 hours prior to predicted high tide, showing that *L. s. angulifera* tend to release spawn on the outgoing tide. At different seasons the time of the highest tide varies. During summer, highest spring tides occurred in the afternoon from approximately 1200 to 1500 hours, but during the fall the highest spring tides fell from midnight to 0300 hours. During the end of October and the beginning of November the spawning times of a group of 24 females (from the marsh grass colony) were found to correlate with the time of the highest tide for the date, even though the time differed approximately 12 hours from the highest tides during the summer. Apparently, it is the tide and not the time of day that determines the time of spawn release in this species. Note that this rhythm was manifest in individuals collected 1-2 days before spawning and held in aquaria for 5-6 days without tidal stimulation. Note also that in the Gulf of Mexico tides are considered diurnal at some seasons in that only one tide produced discernable changes.

Observations on *Littorina scabra angulifera* on the seawall showed that spawning occurred there on the outgoing flood tide also. These snails have been seen migrating downward toward the water as the tide begins to recede so that there is a concentration of snails within 6 cm of the waterline. It was among these animals that spawning females could be found although males also migrated downward at this time. A detailed study of the vertical migrations of these snails is the subject of another report.

Spawning in laboratory situations

The results obtained from observations of animals isolated in aquaria indicate that spawn release involves more than just a response to the rise and fall of the water level, and that there may be an endogenous rhythm involved as well in the reproductive process in these animals. Further information regarding this phenomenon was obtained from 2 groups of snails which were kept in the relatively constant environment of an aquarium for 1 complete breeding cycle of 2 weeks. These animals were collected 2-3 days prior to full or new moon; the gravid females were isolated and allowed to spawn. The males and non-gravid females were kept in community aquaria in which shells and rocks covered with algae were placed for feeding purposes. After spawning the females were returned to the community aquaria where the whole group was watched to study subsequent reproductive behavior.

Mating pairs were noted over periods of 11 and 8 days, respectively, considerably longer than the usual 4-5 day peak seen in the field. Of the females in the 2 groups, 78% and 31% produced spawn. Only about 50% of the gravid females in these groups released live veligers. The rest released dead veligers or did not release spawn at all. Spawning started at the date of full or new moon but did not show any tidal periodicity. These females had large numbers of veliger shells in the feces, showing that they had ingested the young. Apparently spawn release was disrupted when animals were subjected to "constant" conditions, but egg production occurred on schedule.

Water deprivation during normal spawning time also disrupted spawn release. Forty-nine gravid females were placed in dry aquaria for the duration of the normal spawning period (approximately 5 days). When spawning for the period was over, as evidenced by completion of spawning in a group of controls, these 49 females were placed in aquaria containing 2-3 cm of seawater. After 5 minutes, 47 of the 49 animals became active and began crawling. The remaining 2 animals never revived. The 47 live active animals began spawning at once, so that within 1 hour 20 individuals (42%) had spawned. After 2.5 hours 28 (59.5%) had spawned and after 12 hours 35 females (74.5%) had spawned. At the end of 60 hours, 42 animals (89%) had spawned. The remaining 5 animals were dissected at the end of 84 hours and veligers were still in them. Veliger shells were found in the feces of these animals also. There was no correlation between tidal periodicity and spawning in these individuals.

In a second experiment on the effects of water deprivation on spawning, 43 gravid female *Littorina scabra angulifera* were placed in dry bowls for 14 days (1 complete breeding cycle). After desiccation, the test animals were returned to water. Twenty-four responded by crawling within 20 minutes; 19 did not respond and were found to be dead. Of the 24 live animals, 11 spawned, most of them within 1 hour after being returned to water. Seven of the animals released some live veligers, but there were many dead veligers among those released. None of the live veligers lived more than 1 day. Only dead veligers were released by the remaining 4 animals. All of these animals contained large numbers of veliger shells in the feces. Thirteen of the surviving animals did not spawn. These were examined approximately 31 hours after being returned to water and no spawn was found in the mantle cavity, but dead veliger shells were found in the feces. Apparently these animals had ingested the young. Examination of the 19 dead animals revealed that they were in varying stages of decomposition, and all of them contained masses of dead veligers in the mantle cavity; there were no veliger shells in the feces.

The mortality (44%) observed in the aforementioned group was exceedingly high for *Littorina scabra angulifera*. Preliminary experiments on water deprivation

showed that mature snails (including males and non-gravid females) displayed only 17.5% mortality after 10 weeks of water deprivation. To examine the apparent increased susceptibility of gravid females to water deprivation, 38 gravid females, 36 males and 13 non-gravid females were placed in aquaria without water for a period of 14 days. Upon being returned to water at the end of this period, it was found that 9 of 38 gravid females never responded and were dead. Of the 29 animals that responded, 4 became moribund in 3 hours and were dead 12 hours later, a 34% mortality in the gravid female group. Of the 36 males, 3 failed to respond and were found dead. None of the 13 non-gravid females failed to respond. Of the 46 responding snails none became moribund; all were surviving several days later. Thus the total mortality in the group of 49 males and non-gravid females was 6.1%. Since the 2 groups were tested simultaneously, differences in temperature or humidity could not be responsible for the difference in mortality. Apparently gravid females were more susceptible to water deprivation than were males and non-gravid females. This could be due to: (1) the effects of desiccation alone, (2) the combined effects of desiccation and the presence of the egg mass in the mantle cavity which could interfere with respiration, (3) the effects of toxic substances released by veligers (dead or alive). The fact that large numbers of veliger shells were found in the feces of live females but not in those of dead females suggests that females which ingested veligers may have prevented the build up of toxic substances and hence survived. In any case, increased mortality of gravid females as compared with males and non-gravid females when deprived of access to water may be a factor in spawn release in this snail.

The results of these experiments show that water must be present for spawn to be released. Water deprivation for 5 days resulted in some loss of viable spawn. The majority of the animals spawned upon return to water, but the daily tidal spawning rhythm was upset. Water deprivation for 14 days, however, resulted in almost complete loss of young since veligers died or were ingested by the female. One third or more of the gravid females died within the 2-week period.

Numbers of larvae released

The number of larvae released by individual females was very large. It was found that between approximately 10,000 and 246,000 veligers were released by a single female in a breeding period. Our data show that the smaller seawall snails (ranging in size from 8.9 to 17.3 mm shell height) released from 9,800 to 43,000 larvae per spawn period. Within this group, the largest did not always release the greatest number of veligers. However, 7 spawns from large (20.0-27.5 mm shell height) *Spartina* marsh females yielded from 71,000 to 246,000 larvae. All but 1 were over 100,000. Apparently these larger animals tend to produce greater numbers of young in 1 breeding period.

Spawning: *Littorina irrorata*

Spawning in this species was not investigated as thoroughly as in *Littorina scabra angulifera* because the process was found to be very sporadic in the Tampa Bay area. Since *L. irrorata* does not brood young in the mantle cavity but releases pelagic egg capsules, spawning was detected by observing females in aquaria. In some instances the gonads were studied to determine if ripe gametes were present, but this method was avoided in order not to deplete the population. Continuous observation of different groups of *L. irrorata* from June, 1971, to mid-July, 1972, revealed that copulation occurred more often than spawning. When spawning was detected it was found to occur during and a few days following full or new moon

dates. It was not observed during all full or new moon periods, however, but only on the following dates:

1971
22 June new moon: 1 of 8 females
6 August full moon: 5 of 15 females
4 September full moon: 2 of 49 females
1972
16 January new moon: 6 of 19 females
28 April full moon: 7 of 26 females
29 May full moon: 1 of 36 females
11 July new moon: 6 of 13 females

The relative numbers of spawning females given above do not reflect the percentage spawning in the population as a whole, since females were selected from copulating pairs where possible. It is possible that spawning did occur in the natural habitat at other times but was suppressed in animals placed in aquaria and therefore not detected. Examination of gonads in some of these instances, however, revealed that ripe eggs had not been produced although sperm were present in the oviduct.

Although spawning was not detected in many of the groups studied, the presence of copulating pairs indicates that reproductive activity did occur. The observations also suggest that there is a bi-lunar periodicity in spawning in this snail similar to that in *Littorina scabra angulifera*. The picture is not nearly as clear-cut, however, and it is possible that spawning did ocur at other times.

Spawning in *Littorina irrorata* was also found to correlate with the time of high tide at a given date (Fig. 3). Of a total of 46 instances of spawn release, 67.4% began from 0.5 hours before to 0.5 hours after time of predicted high tide. In 17.4%, spawning began between 2.5 and 1.5 hours prior to high tide, and in 15.2%, from 0.5 to 2.4 hours after predicted high tide. On dates when tides in the area were diurnal (24 hours - all summer spawning) spawn was released only once during a 24 to 25-hour period, but during the January and April spawning periods, when tides were semi-diurnal, spawn was released at 12 to 13-hour intervals.

Littorina irrorata releases simple, pelagic, bi-convex capsules containing 1 fertilized egg each (Bingham, 1972b). Among hundreds of thousands of such eggs observed, only 1 capsule was seen that contained 2 eggs. At the time of spawning the egg is in the 1-celled stage prior to release of polar bodies. Development proceeds in this capsule to the veliger stage whereupon hatching occurs. The form of the capsule is very simple and resembles that described by Marcus & Marcus (1963) for *L. flava* on the coast of Brazil. The capsules vary in diameter from 0.31 to 0.46 mm, including an outer rim which is approximately 0.028 mm wide. The egg is located in the center of the capsule and is enclosed in an egg covering. The diameter of the egg and egg covering is approximately 0.085 mm; the diameter of the egg alone is approximately 0.071 mm. This size is similar to the dimensions of the egg and egg covering found in *L. scabra angulifera* in this area.

Spawning in *Littorina irrorata* was observed in females isolated in bowls as in *L. scabra angulifera*. Females submerged to release spawn. Body orientation was not important but the shell aperture was always under water. Observation of spawning females in the field revealed that *L. irrorata* spawns under water in the natural habitat, unlike *L. s. angulifera* which relies upon wave wash to supply water necessary for spawning. Spawn release lasted continuously for from 1 to 2 1/2 hours. Individual females released spawn on from 2 to 4 successive days in 1 breeding period. In all samples observed, the first spawning day was always the date of full or new moon. Spawn was seen as a whitish stream emitted from the right side of the shell aperture. Female *L. irrorata* make no spawning motions

as do female *L. s. angulifera*.

Hatching in aquaria occurred in from 27 to 40 hours in eggs that developed at 26-28°C and in 53 to 56 hours in eggs that developed at 22-24°C. The variation in hatching times at a given temperature resulted from hatching at slightly different stages of development, but all hatchlings were swimming veligers.

Observations of hatching young revealed that the embryo breaks out of the egg covering first, then swims actively inside the outer capsule for between 20 minutes and 1 hour, following which it hatches from the central portion of the capsule and begins swimming in the water.

The number of eggs released by female *Littorina irrorata* in spawning was established in the same manner as those for *L. scabra angulifera*. The number of eggs spawned ranged from 15,000 to 32,000 for any one spawning instance, and can be seen to be of a similar order of magnitude as that in *L. s. angulifera*. Bingham (1972b) found 43,000 and 85,000 capsules released per spawning but his animals released eggs over a 2-4 hour period.

Development

The early development of both species of *Littorina* was similar. Both have pelagic veligers which have a planktonic stage before they metamorphose into crawling snails with a supratidal existence. Development in both species was studied in whole live embryos only. No sectioning was done and thus structural details are not available.

In *Littorina scabra angulifera* early developmental stages were studied by removing eggs from the mantle cavity of the female prior to spawning. The eggs were nearly always in 1 stage of development at any given time, which suggests that egg deposition probably occurs only once per breeding period and not on several successive days. This finding is in variance with that of Struhsaker (1966) who reported that *L. s. scabra* (a closely related species) had eggs in several different stages in the mantle cavity at any given time. Development in *L. irrorata*, in the present study, was observed from embryos in pelagic capsules.

Early development of *Littorina scabra angulifera*

The earliest stages of *Littorina scabra angulifera* found were in the 1-celled stage prior to release of the polar bodies. At this stage the egg contained one small clear area; the rest of it was uniformly dense and presumably contained yolk granules. Just prior to polar body extrusion a change in the configuration of the clear area (animal pole) was observed. At that time a polar lobe was seen to form at the vegetal pole opposite the clear area. After polar body extrusion, the clear area disappeared and the egg appeared uniformly dense throughout. When viewed under the stereomicroscope the egg was a pale yellow color. The first cleavage occurred at about 1 1/2 to 2 hours after polar body extrusion and was also accompanied by the formation of a polar lobe, the material from which went into one of 2 blastomeres. At 3 to 3 1/2 hours most eggs were in the 4-cell stage. At this time it was not possible to follow the polar lobe and each of the 4 blastomeres appeared uniform in both size and in the distribution of yolk granules. The third cleavage occurred at 6-7 hours and resulted in 4 small clear micromeres and 4 large yolky macromeres. This cleavage was synchronous, there being no intermediate 6-cell stage as in some mollusks. During subsequent cleavages, the micromeres formed a cap of clear cells on the yolky macromeres. Gastrulation was first evident at 15 hours when 1/2 of the embryo was covered by a cap of clear cells. By 20-27 hours, gastrulation was complete and there was an outer layer of clear cells surrounding an inner mass of yolky cells. At approximately 39-40 hours, the embryos began

TABLE 3. Rate of development in *Littorina scabra angulifera* and *L. irrorata* at an environmental temperature of 26-28°C.

Stage	*L. s. angulifera*	*L. irrorata*
2 cells	1 1/2-2 hours	1 hour
4 cells	3-3 1/2 hours	2 hours
8 cells	6-7 hours	3 hours
16 cells	9-10 hours	3-4 hours
multi-cell or blastula	12 hours	7 hours
gastrulation, start	15 hours	9 hours
gastrulation, end	20-27 hours	hours
early embryo before cilia and rotation	40 hours	11 hours
trochophore, cilia and rotation	50 hours	20 hours
early veliger	66 hours	23 hours
veliger shell and vela obvious	72 hours	26 hours
veliger with operculum and foot	88 hours	30 hours
hatching	96-100 hours (4 days)	27-40 hours

to assume a triangular shape but neither cilia nor rotation were evident. By 50 hours the embryos had become ciliated and were rotating within the egg covering. They had a distinct triangular shape and could be termed trochophores. At 62 hours the shape was more pronounced and rotation more rapid. By 66 hours the embryos were early veligers. A ciliated foot and operculum were evident at 76 hours. At 88 hours the diameter of the egg covering had increased from 0.085 mm to a range of 0.114-0.128 mm, thereby allowing the veligers to swim freely within the covering. No statocysts were visible at this time, although they were present at hatching or soon thereafter. Hatching occurred at 96-100 hours.

Early development of *Littorina irrorata*

Development in *Littorina irrorata* is similar to that in *L. scabra angulifera*, the major difference lying in the rate of development. The polar lobe in *L. irrorata* is larger than in *L. s. angulifera* and can be followed into one of 4 blastomeres. The egg of *L. irrorata* appears less dense but is approximately the same size as in *L. s. angulifera* and has a whitish rather than a yellow color. Table 3 gives the comparative chronology of the developmental stages in the 2 species.

In most instances, hatched veligers of both species in the present study did not live for more than 2-3 days, due possibly to lack of food, over-crowding, or attack by microorganisms. One group of *Littorina irrorata*, however, lived for 4 days after hatching. During this time eye spots developed lateral to the statocysts which were present at or soon after hatching. There were no pigmentation or other features to distinguish the 2 species in the veliger stage.

DISCUSSION

This study and that by Lenderking (1954) show that *Littorina scabra angulifera* displays reproductive periodicities similar to those shown by other *Littorina* (Fretter & Graham, 1962; Struhsaker, 1966; Borkowski, 1970). In addition, the present

study demonstrates that the cycle of egg production is apparently endogenous since female snails produced gametes "on schedule" when kept in the relatively constant environment of an aquarium for 2 or 3 weeks. Spawn release, however, was disrupted in such animals and was prevented in females while deprived of water. Apparently a combination of endogenous factors and external environmental conditions such as abundant moisture and tidal stimulation is necessary for reproductive success in this species. This insures placement of the planktonic young in an environment favorable for both survival and dispersal.

Copulatory behavior in both species was seen to follow both a bi-monthly and a daily tidal periodicity. Observations of workers other than Lenderking (1954) do not show distinct cyclical rhythms of copulation in *Littorina* but indicate that copulation occurs whenever moisture is abundant (Gibson, 1964; Struhsaker, 1966). Possibly the apparent correlation between mating activity and lunar or tidal phase reflects differences in humidity so that mating is more closely correlated with this factor. Our observations of *L. scabra angulifera* and *L. irrorata* in laboratory aquaria tend to support such a view since copulatory activity there occurred without regard to tidal or lunar periodicity and animals in dry aquaria did not copulate.

Our results and those of Linke (1934), Gibson (1964) and Struhsaker (1966) indicate that it is the males that seek partners since female-female pairs were not formed. Interspecies mating has also been reported in other littorines by Linke (1934) and Struhsaker (1966). The mechanism by which pairs form and the factors initiating mating behavior were not investigated in this study, although it was noted that snails tend to follow exactly the trails of other snails. Recently Dinter & Manos (1972) have shown evidence of a chemical attractant (pheromone) in *Littorina littorea*. In any case it is evident that contact with another *Littorina* by the male will induce mating behavior if conditions are proper.

Descriptions of copulation in littorinids have been given by Hayes (1929), Linke (1934), Fretter & Graham (1962), Marcus & Marcus (1963), Gibson (1964), Struhsaker (1966) and Bingham (1972b). Our observations of the process in *Littorina scabra angulifera* and *L. irrorata* concur with their observations and show that the process is similar in all species.

The sporadic nature of spawning and lack of newly recruited *Littorina irrorata* indicate that reproduction was not successful for this species in the Tampa Bay area during the 13 month study period. Since this location is near the extreme southern limit of the range of *L. irrorata* (Bequaert, 1943), it is probable that conditions are not optimum but just sufficiently favorable for it to survive. Climatic factors such as temperature, humidity and possibly day length are doubtless factors bearing on reproduction in this species.

Spawning in *Littorina scabra angulifera* was shown to be markedly seasonal in the Tampa Bay area, with the peak months corresponding to the warm, humid summer season. This same species has been shown to spawn throughout the year in the Miami area (Lenderking, 1954) and only in July and August in Bermuda (Lebour, 1945). Spawning in *L. littorea* has also been shown by Smith & Newell (1954) to be seasonal, with the peak spawning season varying with geographical location. They concluded that spawning was dependent upon water temperature, occurring whenever favorable. Since the spawning season in *L. s. angulifera* also varies with geographical location, it is evident that climatic factors (probably temperature and humidity) are involved in initiating reproductive activity in this species.

Embryonic stages of *Littorina scabra angulifera* were not released by any females observed in this study, nor did any individual release spawn on more than 1 day of a breeding period. This is at variance with Lenderking's (1954) observations on *L. s. angulifera* in the Miami area; there embryonic stages were regularly released during the first part of the spawning period and individual females

commonly released eggs on more than 1 day of any breeding period. It is not known whether such differences are adaptive or merely chance variations. Since this is a highly variable snail as regards shell sculpture and color (Rosewater, 1970), perhaps physiological variations also exist.

Littorina scabra angulifera in the Tampa Bay area were similar to those studied by Lenderking (1951) as regards size differences between sexes and the number of young produced per breeding period (Lenderking, 1954). These data indicate that *L. s. angulifera* produces more young than many other littorine species reported (Hayes, 1929; Struhsaker, 1966; Borkowski, 1970).

Our observations show that during the peak breeding season individual *Littorina scabra angulifera* females can spawn in 2 successive breeding periods. Lenderking (1954) has shown, however, that in the Miami area this species does not spawn in 2 successive breeding periods. The average percentage of gravid females per breeding period in the Miami area was approximately 33% with higher percentages in the spring and fall months. Only on 2 occasions in that area did more than 50% of females sampled prove to be gravid. In the Tampa Bay area during the peak breeding months, the percentage of gravid females was frequently over 50% and was 97% in 1 instance (Fig. 2). This was offset by no detectable spawning during the months of December through March so that the incidence of gravid females was approximately 20% per breeding period when averaged over the course of 1 calendar year. Viewed in this manner, it is seen that *L. s. angulifera* in the Miami area have a higher total biotic potential than those in the Tampa Bay area.

Spawning in *Littorina scabra angulifera* continued later into the fall in animals in a marsh grass habitat than in those on a seawall. It was also found that the larger animals from the natural habitat produced more spawn per individual female than did those from the seawall. In the case of *L. irrorata*, spawning was detected in animals from both habitats but no conclusions as to differences in reproductive potential could be reached. However, *L. irrorata* from the marsh grass habitat were larger than those on the seawall. These data may indicate that the natural habitat of marsh grass and mangrove is an environment more favorable to these species than is a seawall.

The development time from fertilized egg to swimming veliger varied greatly in the 2 species studied. *Littorina scabra angulifera* took approximately 4 days. This time is comparable to that taken by *L. picta* and *L. pintado* (approximately 3 days) in Hawaii (Struhsaker, 1966). Development of *L. irrorata* was extremely rapid, however, there being no recorded instances of such rapid development in other species of *Littorina* (Struhsaker, 1966). Again this rapid development at summer temperatures (26-28°C) probably reflects the fact that *L. irrorata* is essentially a warm temperate rather than a tropical species.

Our observations revealed that the details of early development in both species and the sizes of developing eggs and embryos are very similar. There is no detectable difference between the newly hatched veligers, and there are no distinguishing features such as pigmented areas which would identify them as *Littorina* veligers in the plankton. Struhsaker & Costlow (1968), studying larval development of 3 Hawaiian littorines (*L. picta*, *L. pintado* and *L. scabra scabra*) in the laboratory, reported that the right velar lobe and tentacle are larger than the left velar lobe and tentacle in all 3 species. Such size differences were not seen in newly hatched *L. s. angulifera* or *L. irrorata* veligers. No rearing of the larvae has as yet been attempted; thus it is possible that these features might appear during subsequent larval development.

SUMMARY

1. Factors affecting the reproductive process in *Littorina scabra angulifera* and

Littorina irrorata, which occur sympatrically in the Tampa Bay, Florida, area, are described. Both lunar and daily tidal periodicities in the reproductive process of both species were found. Spawning began at full or new moon times and continued for approximately 4-5 days. Spawn release was also correlated with the time of high tide.

2. *Littorina scabra angulifera* releases swimming veligers and does so only once per breeding period of each individual. *L. irrorata* releases 1-celled eggs in simple bi-convex capsules and does so over a period of 2-4 days per breeding period of each individual.

3. *Littorina scabra angulifera* was found to spawn mainly during the months of June-November in this study area. Spawning by *L. irrorata* was sparse and sporadic. Most instances occurred during spring and summer. Copulation was noted, though rarely, during some winter months and 1 instance of spawning occurred in January.

4. The effects of a relatively constant indoor aquarium environment were found to disrupt but not stop reproductive activity in both species. *Littorina scabra angulifera* produced spawn but the release of larvae was disrupted so that no or only reduced numbers of veligers were produced. In *L. irrorata* only the male produced gametes so that although copulation occurred, the females did not release eggs.

5. The effects of water deprivation on spawning in *Littorina scabra angulifera* were studied. It was found that females could not release larvae unless water was present. When water was provided after varying periods of deprivation, it was found that some loss of viable spawn occurred and that the daily tidal rhythm was disrupted. Gravid females were shown to be more susceptible to water deprivation, in terms of mortality, than were males and non-gravid females.

6. *Littorina scabra angulifera* from marsh grass habitats were found to be larger and to produce more spawn than those from the seawall. They also spawned 1 month later into the fall than did seawall snails. Occasional spawning was detected during the winter in marsh grass snails although none was found then in seawall animals. This suggests that the seawall is a less favorable environment for *L. s. angulifera* than a *Spartina* marsh.

7. The early development from the fertilized egg to the swimming veliger larvae was described in both species and found to be similar. At 26-28°C development from fertilized egg to hatched veliger took 4 days for *Littorina scabra angulifera* and 27-40 hours for *L. irrorata*. A table giving the comparative chronology of the developmental stages is included.

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RELATIONSHIPS OF EURASIAN-NORTH AFRICAN *ANCYLUS* TO THE NORTH AMERICAN *RHODACMEA* (PULMONATA: ANCYLIDAE) AS SHOWN BY APICAL SHELL SCULPTURE[1]

J. B. Burch

ABSTRACT

A Scanning Electron Microscope was used to study the apical shell sculpture of various freshwater limpets, and especially to compare *Ancylus* with *Rhodacmea* and to compare these 2 genera with other Ancylidae. The apical sculpture of *Ancylus* and *Rhodacmea* are nearly identical in basic details, indicating that the 2 genera are probably more closely related than many workers have suspected in the past. The apical shell sculpture of *Burnupia, Ferrissia, Laevapex* and *Uncancylus* are basically different from the sculpture seen in *Ancylus* and *Rhodacmea*.

INTRODUCTION

The Scanning Electron Microscope (SEM) has been a big advance in elucidating the fine surface detail of biological structures. Its recent use with the Ancylidae (Burch & LoVerde, 1974) has confirmed that the apical sculpture of freshwater ancylid genera is an important taxonomic character, as advocated long ago by Walker (1902, 1903, 1912). The purpose of this paper is to describe in detail the apical sculpture of the Eurasian-African *Ancylus fluviatilis* and to compare this species' apical sculpture to that of species of other ancylid genera and especially to the North American *Rhodacmea*, with which *Ancylus* has previously been suggested to be related by other characters (e.g., see Burch, 1962a, b).

METHODS AND MATERIALS

Shells of freshwater limpets were cleaned by immersing them in sodium hypochlorite (commercial "Clorox"), removing the periostracum and rinsing the shells in distilled water. The shells were then dried and glued with Duco cement or aluminum paint to the holder to be used in the SEM. The shells were coated with gold in a vacuum evaporator by ionizing radiation and viewed and photographed with a JEOL (Ltd.) JSM-U3 Scanning Electron Microscope. Photographs were taken at 100X, 200X, 300X and 600X with Polaroid P-51 P N film.

The 2 populations of *Ancylus fluviatilis* Müller used in this study were from (1) a spring at the Hydrobiological Institute, Ohrid, Yugoslavia and (2) headwaters of Oued Rdat, near Tizin-Tichka Pass, Atlas Mts., Morocco (?*strigatus* Bourguignat 1853). The *Rhodacmea* species used for comparison with *Ancylus* were (1) *R. filosa* (Conrad), Tallaseehatchee Creek, 4 miles above Childersburg, Talledega County, Alabama, U.S.A. and (2) *R. rhodacme* Walker, Coosa River, Leoto Shoals, St. Clair County, Alabama, U.S.A. The other species illustrated here to show the contrasting types of apical shell sculpture found in the Ancylidae are (1) *Burnupia capensis* Walker, Escomba, Natal, South Africa, (2) *Laevapex diaphanus* (Haldeman), Tennessee River at Knoxville, Tennessee, U.S.A., (3) *Ferrissia rivularis* (Say), Tennessee River at Muscle Shoals, Tennessee, U.S.A. and (4) *Uncancylus concentricus* (d'Orbigny), Brook in Ozorio, Rio Grande do Sul, Brazil.

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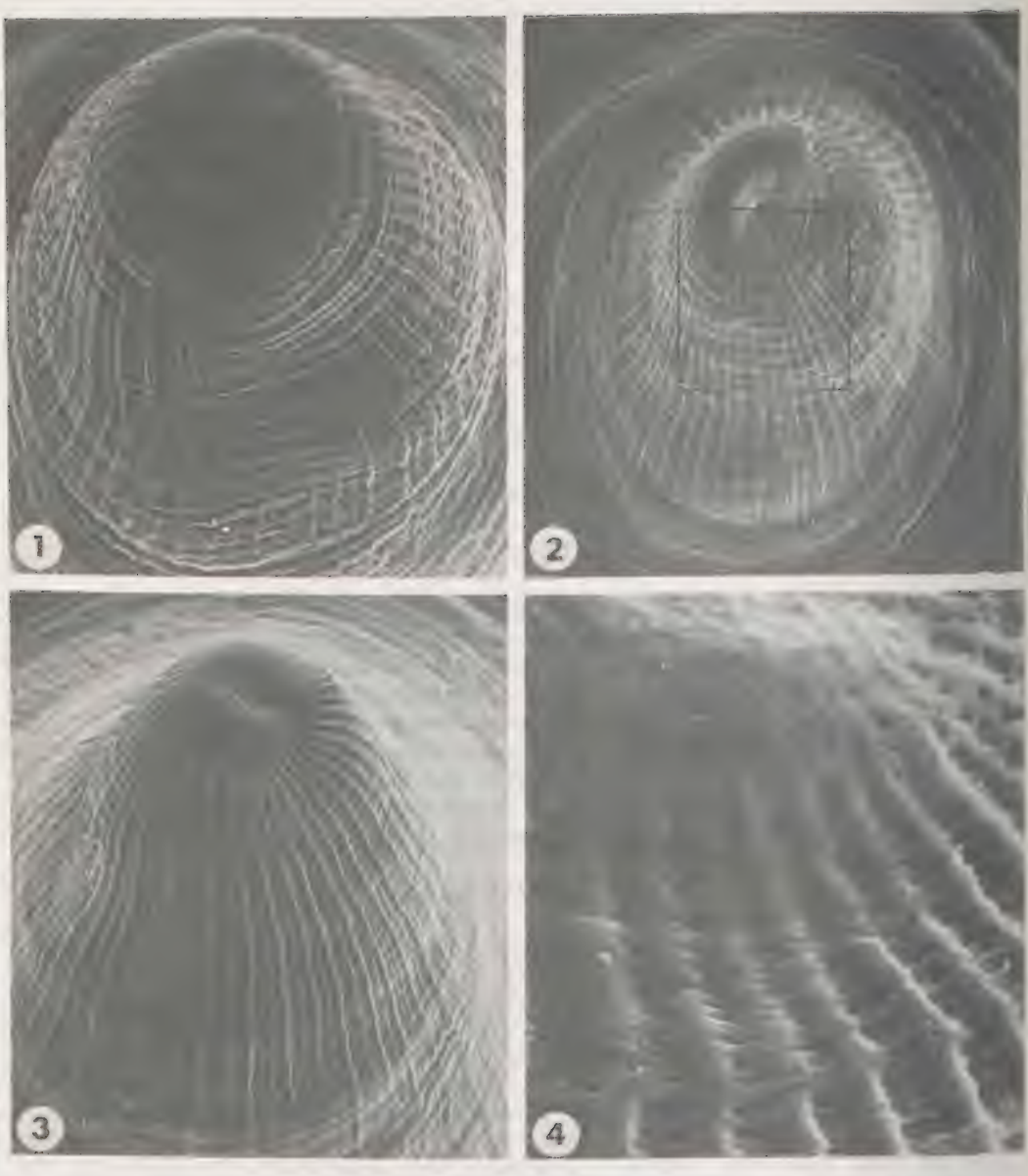

(FIGS. 1-12 are photographs taken with the Scanning Electron Microscope of the shell apices of freshwater limpets. FIGS. 2, 5-9 are reproduced from Burch & LoVerde, 1974.)
FIG. 1. *Ancylus fluviatilis,* Ohrid, Yugoslavia (ca. 74X). FIG. 2. *Rhodacmea rhodacme,* Coosa River, Alabama, U.S.A. (ca. 74X). FIG. 3. *Ancylus fluviatilis,* Oued Rdat, Morocco (ca. 74X). FIG. 4. *Ancylus fluviatilis,* enlargement of area marked in Fig. 3 (ca. 444X).

OBSERVATIONS

The Apical Shell Sculpture of *Ancylus* and *Rhodacmea*

Ancylus fluviatilis (Fig. 1)

In the Macedonian specimens, the exact center of the apex is nearly smooth ex-

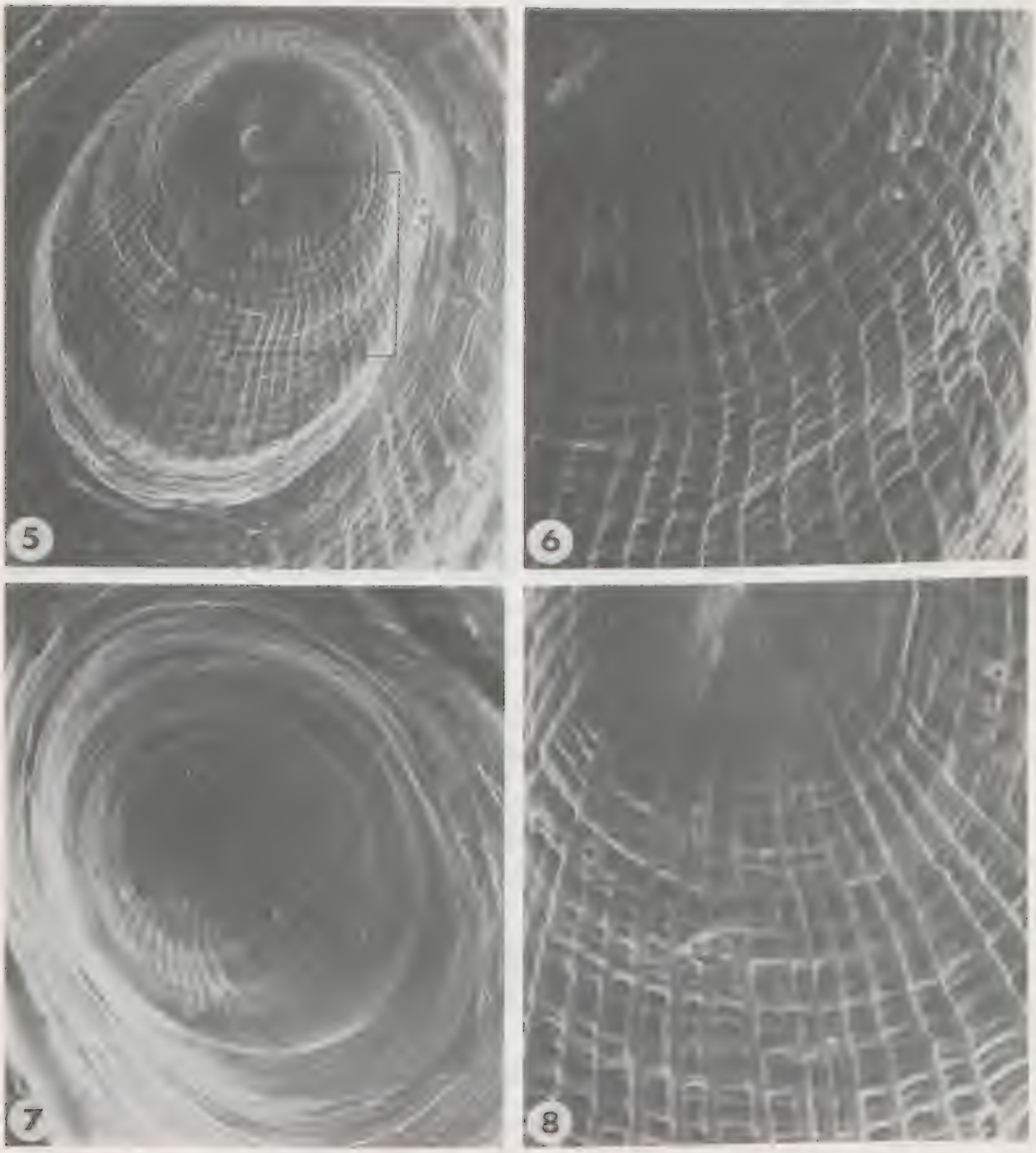

FIG. 5. *Rhodacmea filosa,* Tallaseehatchee Creek, Alabama, U.S.A. (ca. 74X). FIG. 6. *Rhodacmea filosa,* enlargement of area marked in Fig. 5 (ca. 222X). FIG. 7. *Ferrissia rivularis,* Tennessee River, Tennessee, U.S.A. (ca. 148X). FIG. 8. *Rhodacmea rhodacme,* enlargement of area marked in Fig. 2 (ca. 222X).

cept for a central pit, which seems to be characteristic of all freshwater limpets. About 0.2 mm from the center of the apex a distinct and patterned sculpture begins, starting weakly but rapidly becoming prominent. The pattern consists of radial ridges or cords, crossed perpendicularly by less prominent transverse ridges. The radial ridges, although slightly disrupted at the juncture between the embryonic and post-embryonic shells, continue to the apertural edge of the shell, diverging distally as the shell enlarges. As the radial ridges diverge, new radial

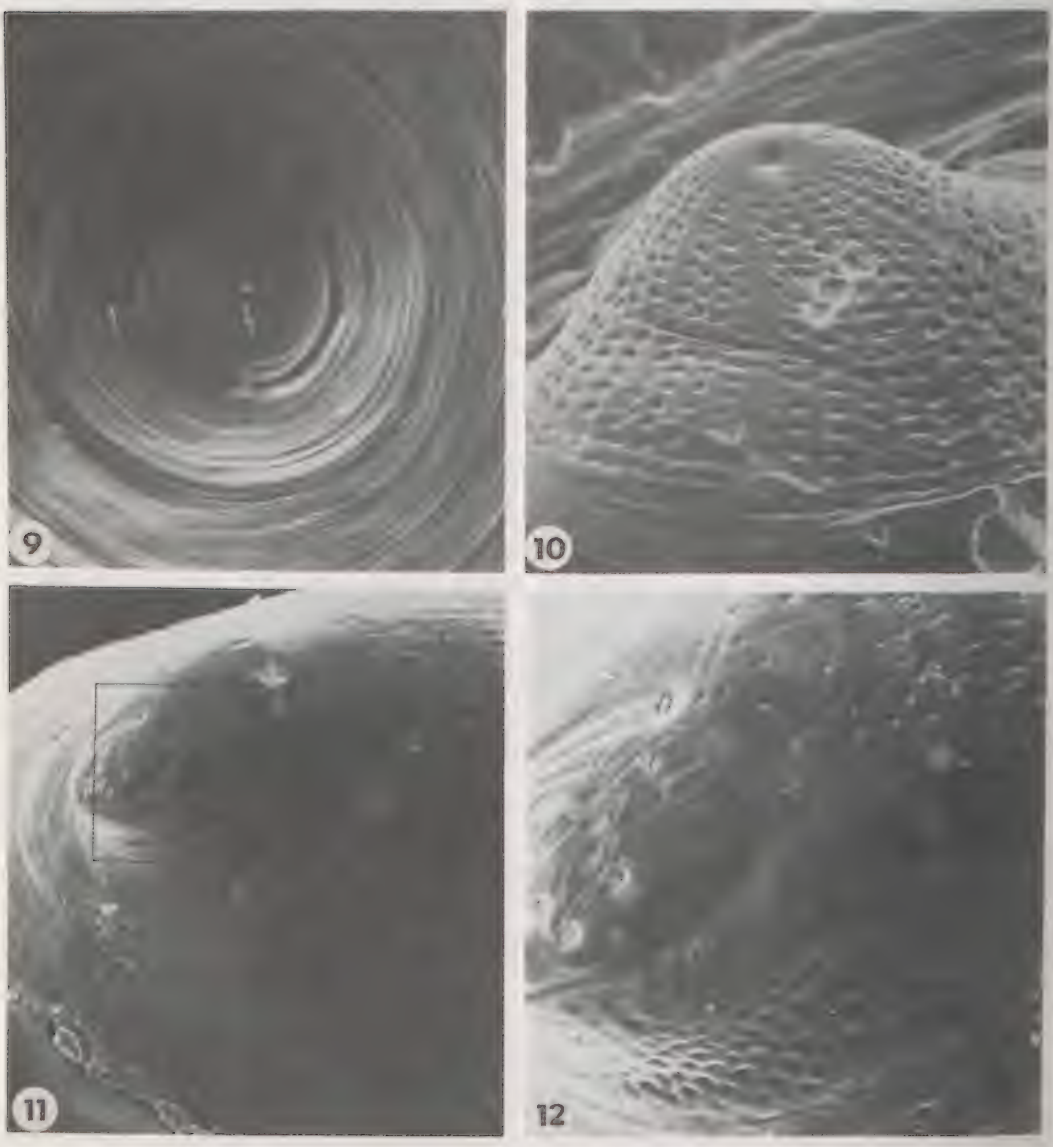

FIG. 9. *Laevapex diaphanus*, Tennessee River, Tennessee, U.S.A. (ca. 74X). FIG. 10. *Burnupia capensis*, Escomba, South Africa (ca. 148X). FIG. 11. *Uncancylus concentricus*, Ozorio, Brazil (ca. 74X). FIG. 12. *Uncancylus concentricus*, enlargement of area marked in Fig. 11 (ca. 222X).

ridges emerge, which do not become as prominent as the original radial ridges. Near the apex, the radial ridges have a very slight sinistral spiral. The transverse ridges ("growth lines") are very closely spaced apically, but gradually become more widely spaced as the shell gets larger.

The apical tip of the embryonic shell has a "dimpled" or "pushed-in" appearance.

Ancylus fluviatilis (*?strigatus* Bourguignat 1853) (Figs. 3, 4)

The shell sculpture of this North African population is nearly identical in all basic details to that of their Ohrid spring relatives, as can be noted by comparing Figs. 1 and 3 (Fig. 3 is at a more oblique angle than Fig. 1).

Rhodacmea filosa (Figs. 5, 6)

The apical tip of the shell is irregular and somewhat malleated, but otherwise lacks sculpturing. About 0.1 - 0.2 mm radially from the exact center of the apex, a more distinct patterned sculpture begins. This sculpture is weak at first, but rapidly becomes prominent. The strongest part of the pattern consists of radiating ridges, initially more or less parallel and then diverging distally, where new weaker radial ridges emerge. The radial ridges continue distally to the apertural edge of the shell. The radiating ridges are crossed perpendicularly by lower, thinner concentric transverse ridges.

Rhodacmea rhodacme (Figs. 2, 8)

The apical sculpture is nearly identical to *Rhodacmea filosa*, but the ridges stop about 1.0 - 1.3 mm from the apical scar, instead of continuing to the shell margin.

The Apical Shell Sculpture of Other Ancylid Genera

Of the species listed above, the simplest apical shell sculpture is seen on *Laevapex diaphanus* (Fig. 9). It is generally smooth (and previous to SEM observations was considered to be entirely smooth), but under high magnification a very weak, hardly visible, sculpture of extremely shallow, radiating grooves may be seen. This would appear to be the remnant of a once stronger apical sculpture of radiating ridges and grooves, such as found in *Ferrissia* (Fig. 7). Crossing the obsolescent radial sculpture in *Laevapex* are concentric, irregularly spaced "growth" wrinkles. In *Uncancylus concentricus* (Figs. 11, 12) the apical region is smooth, but about 0.3 - 0.4 mm from the apical pit or "scar" is a circular band of about 0.3 - 0.5 mm wide of closely spaced shallow pits. *Burnupia capensis* (Fig. 10) also has pits, or punctae, but they are quite basically different from those in *Uncancylus*. They begin near the apical pit, are deep and more definitely spaced, extending downward on the shell radially for about 0.7 mm. In *Ferrissia* radiating grooves begin near the apical pit and extend for about 0.6 mm, where they fade out. As they diverge distally, new grooves appear before the ridge between the grooves gets very wide.

DISCUSSION

Until rather recently, a particular relationship between *Ancylus* and *Rhodacmea* had not been suspected. But, in 1960, Basch mentioned that, "several features, such as the shape of the jaw, the radular sac and the albumen gland seem to indicate an affinity [of *Rhodacmea*] with the genus *Ancylus*," but added that "...these resemblances may be superficial and coincidental." Burch (1962a, b) grouped the 2 together in the same subfamily because they shared certain common characteristics; for instance, they both had the same easily distinguishable continuous reversed-C adductor muscle attachment to the shell, which differed from all other freshwater limpets, except *Ancylastrum* (the latter now placed with Planorbidae by Hubendick, 1964). Further similarities were noted between *Ancylus* and *Rhodacmea* in shell, radula[2] and base chromosome numbers. Basch (1963) noted that

[2]In *Ancylus* the beginnings of the peculiar splitting of the lateral radular teeth into widely divergent mesocones and ectocones, a condition greatly developed and exaggerated in *Rhodacmea*, can be seen (see pl. 2, fig. 3 by H. B. Baker in Walker, 1925).

"...ancylid snails appear to fall into two major groups...," one of which "...includes *Ancylus* and *Rhodacmea*, in which the shell, animal, and habitat are quite similar, and the radula shows some similarity (particularly in the marginal teeth)." He further speculated that "...on distributional grounds [*Rhodacmea*] appears to be an isolated derivative from an *Ancylus*-like ancestor..." (see also his fig. 20). Hubendick (1964), on the other hand, stressed "the important anatomical differences between *Ancylus*...and *Rhodacmea*" (p 64) in arguing against placing them together.

The apical sculpture of *Ancylus* and *Rhodacmea*, as elucidated here by SEM, seems to be another indication that the 2 genera are related, each closer to the other than to other ancylid genera. The shell apices of both are not only very similar, but in basic aspects identical, yet their apices differ from all of the other ancylid genera that have been studied.

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BRIEF COMMUNICATIONS

NOTES ON THE SPAWNING AND HATCHING OF THREE SPECIES OF MARINE GASTROPODS.[1] – Specimens of *Distortrix cancellinus*, *Nassa dorsata* and *Hydatina velum* were collected from the Porto Novo coast during January 1971 and February 1972, from trawl catches at a depth of 15-20 fathoms. In the laboratory the snails were placed in glass troughs with aerated seawater that varied in salinity from 30-35‰ and in temperature from 27-31°C.

I. *Distortrix cancellinus* (Roissy) (Prosobranchia: Cymatidae). Information on the spawning and development of tropical gastropod species is sparse. Important works related to this subject in the family Cymatidae are: Anderson's (1959) studies on the egg masses and early life history of *Cymatilesta spengleri* (Perry) from Australian waters, D'Asaro's (1969) studies on embryogenesis and early organogenesis of *Distorsio clathrata* (Lamarck) from Florida, Houbrick & Fretter's (1969) account of the egg masses of *Cymatium nicobaricum* (Röding) from Hawaii, and Gianapati & Sastry's (1973) account of the egg masses of *Cymatium pileare* (Linnaeus) from Indian waters. Spawning and hatching of *Distortrix cancellinus* have not been previously described.

Distortrix cancellinus is a relatively common gastropod species of Indian waters, although it is more common in the tropical Indo-Pacific regions. Specimens were collected during February 1972. They were kept alive under laboratory conditions for several weeks and during that period they began to spawn (Fig. 1).

Distortrix cancellinus laid eggs in the laboratory from February to May. They did not spawn during January or June to August in the laboratory, and egg masses have not been found in the field during these months. Copulation was not observed. All egg masses were deposited on the sides of the glass trough. The temperature and salinity at the time of spawning ranged from 28-31°C and from 32-35‰ respectively.

Ten egg capsules were laid in curved rows parallel to one another (Fig. 1). They laid from 70-80 such rows (mean 76) with 10-20 (mean 16) capsules per row. The egg masses were light yellow, opaque and measured (average) 9 x 2.5 cm. As each ovum contained from 17-22 embryos (mean 20), the egg masses comprized from 22,000 to 26,000 embryos. The diameter of the capsules ranged from 1 to 1.2 mm (mean 1.1).

The spawning process is more or less the same as that observed by D'Asaro (1969) for *Distorsio clathrata*. The egg masses of 4 individuals were selected for examination of egg capsule production. On the average, 1200 capsules (per snail) were produced in a period of 24 hours, i.e., about 1 every 1 1/2 to 2 minutes. The animal is capable of laying continuously for about 2 hours, i.e., of producing 60-74 capsules at a stretch.

As in *Distorsio clathrata* (D'Asaro, 1969), the egg capsules of *Distortrix cancellinus* undergo a series of color changes related to the acquisition of embryonic pigment. Freshly laid capsules are yellow; they gradually turned yellowish-white when nearing the 5th day and then became pure white at the time of hatching, which occurred on the 16th or 17th day. The egg capsules hatched out as veligers. At that time the average diameter of the veliger shell was 2.1 mm. Actively swimming veligers lived in the laboratory for 2-3 days.

II. *Nassa dorsata* (Röding) (Prosobranchia: Nassidae). *Nassa dorsata* (Röding) is a common species found in and around Porto Novo along the coast. Specimens were collected during January 1971. The snails were kept in aquarium tanks and glass troughs until August, with frequent changes of aerated sea water. The egg capsules and development of various species of Nassidae are known from the works of Lamy (1928), Ankel (1929), Lebour (1931, 1937) and Vestergaard (1935). However, observations on the spawning and hatching of *N. dorsata* have not been published previously.

Nassa dorsata laid eggs in the lab from January to May, with the peak season (during which more than 80% of the females engaged in egg laying) falling between mid-February and April. During this period, the salinities and temperatures fluctuated between 30‰ and 35‰ and 27-31°C respectively. Copulation was not observed.

The egg laying process was observed in the aquaria on several occasions. The snails preferred to lay their eggs on the sides of the glass trough. The egg masses were opaque dull-white and measured (average) 7 x 5.5 cm. Ten egg masses of 10 individuals were selected for examination. The pattern of arrangement of the egg capsules was the same as that described for *Nassa costata* Adams (Natarajan, 1957). The egg capsules were laid in curved rows more or less parallel to each other. The time taken for depositing a single egg mass varied from 3 to 4 1/2 hours. Approximately 178 rows were produced by 1 snail in a period of 4 hours, or about 1 row every 1 1/2 minutes. The total number of rows per mass ranged from 138-178, with an average of 158. The number of egg capsules per row ranged from 24-28, with an average of 26, and the total number of capsules per mass ranged from 3500-4600, with an average of 4000.

The egg capsules were more or less triangular (bell-shaped) in outline. They were attached to a broad central ribbon by a thin stalk and distally from a broad edge at the top. The wall of the capsule was smooth, thin and glossy. In shape and by having 1 embryo per capsule, the egg masses of *Nassa dorsata* resembled those of *N. costata* Adams and *N. thersites* (Bruguière) (Natarajan, 1957). The average length and width of 50 capsules measured were 0.51 mm and 0.36 mm respectively.

The ova were light brownish, spherical and their average diameters were 0.18 mm. The hatchlings emerge at the veliger stage in 3-4 days. Just at the time of hatching, the veliger rotates vigorously on its axis and comes into contact with the broader part of the egg capsule which is pushed outward to expand like a balloon. The veliger then quickly pierces the capsule with a jerk. The tip of the veliger shell and the veliger's head, facing the inside of the capsule, come out last.

The newly hatched veligers measured on the average 0.32 mm in length and 0.27 mm in width. The outer lip of the larval shell was prominently extended in the middle, forming a more or less beak-like projection.

The well developed velum denotes long pelagic life for the larva. The veligers lived in the laboratory for 7 days. Their growth was very rapid for the 1st 3 days after hatching, when they showed a sharp increase in length (from 0.35 to 0.44 mm) and width (from 0.27 to 0.36 mm). From the 4th day onwards growth was steady, with a gradual increase of both length and width. The length and width were almost equal on the 6th and 7th days. Unfortunately all the veligers died at this stage and thus no further measurements were possible.

III. *Hydatina velum* (Gmelin) (Opisthobranchia. Hydatinidae). *Hydatina velum* is the only common hydatinid found along the Porto Novo coast during the warmer months. There is no previous report on the spawning and hatching of any species of the genus *Hydatina* from Indian waters, except for a report on the egg mass of *H. velum* by Gravely (1942) from his Madras beach collections. However, the breeding and spawning habits of species in other families of the order Cephalaspidea are available from the works of Hamatani (1961) (Philinidae), Marcus (1972) (Acteonidae) and Kasinathan & Ramamoorthi (1972) (Atyidae).

Specimens of *Hydatina velum* were collected during February 1972. The animals usually remained alive for a week to 10 days, after which they all died. On almost all occasions they spawned at night or in the early morning.

Hydatina velum apparently breeds from March to June, since those are the only months that we have observed egg masses from field collections. Copulation was not observed. The eggs are laid in a long whitish, translucent gelatinous ribbon which is folded to give an irregular contorted, rather circular, appearance (Fig. 2). The egg masses measured about 8 cm in diameter. At the time of spawning, the water temperature ranged from 28-31°C and the salinity from 32-35‰. Ten egg masses of 3 individuals were selected for closer observation and for examination of capsule production. The eggs were massed together like bunches of grapes. The total (wet) weight of a single egg mass varied from 9 to 10.5 gm. On the average, 300 mg of egg mass contained about 3800 capsules. The total number of capsules per mass ranged from 114,300 to 133,350. Egg laying in this species was very rapid, a complete egg mass being laid in a period of about 2 hours.

The egg capsules were granular, colorless and transparent. The number of embryos contained in each capsule ranged from 25 to 30, with an average of 28. Since the total number of capsules per mass varied from 114,300 to 133,350, the material examined contained from 3.2 to 3.7 million embryos per mass. The diameter of the capsule ranged from 0.30 to 0.45 mm, with an average of 0.40 mm. Veligers hatched out in about 8-9 days. The average diameter of the egg and the veliger shell measured 56 μ and 70 μ respectively. The larval shell was transparent and smooth. The veligers lived in the laboratory for 2-3 days.

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FIG. 1. *Distortrix cancellinus* spawning.

FIG. 2. Egg mass of *Hydatina velum*.

NECROPHAGOUS HABIT IN *OPEAS GRACILE* (STYLOMMATOPHORA: SUBULINIDAE).[1] — *Opeas gracile* (Hutton), a pulmonate gastropod belonging to the family Subulinidae (Thiele, 1931), is one of the commonest land snails occurring in India. It is found in abundance in gardens in Calcutta during the rainy season, when aestivating individuals burst forth from the subsoil to resume activity. In spite of the seasonal abundance of this snail, very little is known about its ecology and life history. To study these aspects, we have for some time undertaken extensive field and laboratory observations of this species.

On 16 August 1972, one of us (S. K. B.) noticed 3 *Opeas* snails kept in a jar devouring the soft portions of a dead individual. This surprised us in view of the known herbivorous habit of this and various other species of *Opeas* (Pilsbry & Bequaert, 1927; Graham, 1955; Karlin, 1956). To confirm the above observation, we killed 1 snail on 6 September 1972 and offered it to 5 individuals kept in a separate jar with their normal plant food. The next morning all the soft parts of the dead snail were missing. A week later on 13 September 1972, another dead snail was attacked by live individuals and eaten. A juvenile was seen on 5 October 1972 feeding on another dead juvenile. After nibbling at the muscles for about 7 minutes, this snail retired to another corner of the jar. We then retrieved the dead snail to examine how much of it had been eaten. After 5 minutes the live snail returned to the place where the dead snail had been and, finding it missing, went back to its retreat. When the dead snail was replaced in the jar, this individual again came to it and nibbled at it for about 2 minutes before withdrawing.

On 1 October 1972, 4 specimens were placed in a clean glass jar without any food or soil. Six days later one of the individuals died. Its soft parts were consumed by the survivors, but its eggs were left untouched. We did not notice any aggressive activity or attacks upon each other when several individuals were kept together on starvation for many days. Even when 30 specimens were kept for 10 days in a small jar with some soil but without plant food, there was no indication of attacks upon each other in spite of overcrowding and starvation.

To test their behaviour towards other gastropod species, 1 dead specimen of *Succinea* sp. was offered to 3 *Opeas gracile* individuals; they completely devoured it within 6 hours, with brief resting intervals. The same individuals were offered muscles of a dead shrimp (*Macrobrachium lamarrei*) the next day, and within a minute 1 individual attacked it. Others joined the feast later on, continuing to feed for about 1 1/2 hours, after which they left the corpse. Another snail, offered a piece of dead fish (*Mystus* sp.), began eating it within 3 minutes.

In conclusion, *Opeas gracile* (Hutton), in nature, feeds on leaf litter, but as is indicated by our observations, it is not averse to feeding on dead animals, such as other pulmonates (Moquin-Tandon, 1855; Watson, 1915; Hyman, 1967). It is apparently a saprophagous species, not only helping in the breakdown of leaf litter but also attacking soft parts of small dead organisms, thus acting as a scavenger. It does not appear to be predatory.

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* * * *

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BOOK REVIEWS

F. Paetel 1887–1891, 212
Dall, Bartsch and Rehder 1938, 231
H. H. Edmondson 1933, 231
Lange de Morretes 1949, 449
S. Hirase 1934, 232
K. Baba 1949, 104
C. M. Yonge 1949, 410
W. J. Dakin 1952, 448
G. E. and N. MacGinitie 1949, 411

* * * *

NEW GENERA, SUBGENERA, SPECIES, SUBSPECIES AND NAMES

Cerion pauciscultptum, 425
Cerion rehderi, 422
Cerion shrevei, 436
Cerion sisal, 427
Cerion turnerae, 423
Geomelania parvulina, 180
Indopyrgus bonnei, 3
Liguellus, 123
Merrilliana, 179
Taheitia arcasiana abbotti, 187
Taheitia arcasiana cookei, 186
Taheitia soluta, 190
Taheitia tongana, 190
Taheitia turricula laddi, 189
Tomlinitella, 169
Truncatella thaanumi, 165
Truncatella thaanumi insularis, 166; 446

* * * *

SUBJECT INDEX

Biographical Sketches

Adams, C. B., 233
Anthony, John Gould, 81
Couthouy, Joseph Pitty, 33
Cuming, Hugh, 17
Mighels, Jesse Wedgwood, 213
Morse, Edward Sylvester, 129

Catalogue of Families and Genera

Liguus, 117
Truncatellidae, 157

Monographic Studies

Anodonta implicata Say, 109
Busycon coarctatum Sowerby, 405
Lampsilis cariosa Say and
Lampsilis ochracea Say, 145
Scalarinum Species Complex (Umbonis) in the Genus Cerion, 413

Medically Important Mollusks

Conus, 49
Oncomelania quadrasi, 41
Schistosomophora quadrasi, 5

PREFACE

LITERATURE today regarding all phases of the study of mollusks has reached fantastic proportions. More than one thousand titles on various studies appear each year, published in more than two hundred journals, museum bulletins or other publications. Our aim, in this present series, is to bring together in one publication a few such studies which are limited entirely to mollusks. Each number is an entity and may deal with any phase of malacology whether bio-bibliographic or monographic or it may consist of catalogues of families or genera. A convenient number of pages will be grouped to form volumes, the numbers to run consecutively.

Some of the studies covered in this volume resulted from problems that arose during other research. Others, such as the bio-bibliographic sketches, are part of a long range plan to build up a historic background in our field of mollusks. Such sketches serve a double purpose: to save documentary material concerning malacologists which is now available but which may eventually become scattered or lost entirely and to make known the location of type material upon which much of their work was based.

We are dealing with a phylum of the animal kingdom which may have as many as 200,000 species. This number is, of course, an estimate only: even the approximate number will not be known for many years. Many regions, both sea and land, are still far from being fully investigated. Each decade highlights many new areas or new means of approach that result in additions to the known number of these beautiful and interesting animals.

Just what the aqualung may do for the study of marine mollusks is anyone's guess, but in it we have a new aid that can be effectively used for investigating one of the richest and still

one of the most inaccessible areas of the sea— the rock and coral reef zone. Here, at varying depths, we have many mollusks that are seldom, if ever, cast up on the beach. This is also a region in which dredging has been only faintly successful. Not only will many new forms come to light, but, in addition, it may be possible to become better acquainted with the many rare species now recorded from only a few specimens. In this deeper water, mollusks can be studied in their own environment, free from the vicissitudes of the intertidal zone—a place where the collector can observe them only during their most inactive period, mainly at low tide. The prospects ahead are exceedingly bright and even a novice in the field of biology can and very probably will make important contributions to our knowledge.

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Review Number and Index

Supplement to Joseph Pitty Couthouy
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BOOK REVIEWS

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Ernest E. Williams	31 (p. 383)

Occasional Papers On Mollusks

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BOOK REVIEWS

Andre-Pierre Le Dru 1810, 179
Traité de Zoologie 1960, 260

NEW SPECIES AND SUBSPECIES

Cerion klineae, 249
Cerion lewisi, 255
Cerion utowana abbotti, 251
Hemitrochus clenchi, 161
Hemitrochus riveroi, 174
Taheitia orrae, 186
Tellina alerta, 309
Tellina diantha, 323
Tellina euvitrea, 321
Tellina exerythra, 315
Tellina paramera, 311
Tellina probrina, 319

SUBJECT INDEX

BIOGRAPHICAL SKETCHES

Adams, C. B., 21
Goodrich, Calvin, 189
Maynard, C. J., 137

CATALOGUES OF FAMILIES

Viviparidae, 261
Pandoridae, 413

MONOGRAPHIC STUDIES

Lioplax, 1
Hemitrochus, 153
Viviparus, 385

FAUNISTIC STUDIES

Caicos, Turks, Ragged Ids., Cay Sal Bank Ids., 229
Cayman Ids., 345

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PREFACE

THE pollution of our freshwater lakes, ponds, rivers and streams increases at an alarming rate. Within a few years most of our localized endemic genera and species will be only history of what was once the greatest freshwater molluscan fauna of any area in the world. From the Ohio River in the North, and south to the rivers which drain into the Gulf of Mexico east of the Mississippi River there is a remarkable number of endemic species as well as several endemic genera, which are rapidly becoming extinct.

Pollution began as soon as early man first reached this continent, and from this infinitesimal start it has continued at an ever increasing rate. There is little documentation as to the number of species destroyed, as it would be most difficult and costly to make a broad survey with this point in view, but we do know that certain areas, once rich in mollusks, are now completely destitute of these animals.

Pollution of sufficient concentration to initiate the decline of our mollusks had its start about the middle of the past century. Overfarming in the South brought about heavy silting in many of our southern rivers, and at the same time industrial wastes were becoming a serious problem in New England and elsewhere in the Northeast. Now the problem is a pressing one throughout the country.

Pollution is not the only factor contributing to the disappearance of our molluscan fauna. Navigational and flood control dams have contributed their share. As a result of these dams, particularly in the Coosa River in Alabama and in the Tennessee River in Alabama and Tennessee, the once numerous shoals are now covered with many feet of silt-laden water which has had a catastrophic effect upon the endemic shoal-inhabiting populations in these rivers.

In 1834, T. A. Conrad wrote regarding the remarkable *Paludina magnifica* Conrad [now *Tulotoma magnifica* in the Viviparidae, see plate 46]: "A beautiful species, when perfect, occurring in vast abundance on the masses of calcareous rock,

which have fallen from the strata above, into the Alabama River, at Claiborne." Not a specimen lives today nor has one been seen for many years. In 1933, we failed to find this species on the same rocks mentioned by Conrad. The species, however, does still exist in a few of the smaller tributaries and possibly in some stretches of the Coosa River itself, but it would appear to be only a question of time when these colonies will also disappear.

At the time this introduction was written we received a letter from Mr. Herbert Athearn of Cleveland, Tennessee, and quote the following paragraph:

"This past Tuesday [October 12, 1965] I returned to the Coosa to examine the 'progress' on the new Lock 3 Dam. Water has now been raised about 20 feet at its base and this has been sufficient to inundate all the remaining shoals that we have known as 'Ten Island Shoals'. My main work, however, on this day was to do some final collecting on Big Canoe Creek. This stream will be completely inundated by Lock 3 Dam for about one-half mile above Williams. The stream contains such species as *Tulotoma magnifica* and *Apella pyramidatum* in large numbers. Hundreds of live specimens of the latter species were taken as well as several dozen more live *Tulotoma*, probably for the last time here."

Lock 3 Dam is at Ten Island Shoals, St. Clair Co., Alabama, about 10 miles ESE of Ashville.

Regardless of what is done, even in the immediate future, to clear up the pollution, it cannot bring back the many endemic species which once existed and have been destroyed. Flood control and water storage dams are certainly necessary to meet the demands of an increased population, but they will have a profound effect upon the fauna in our freshwater systems. Unfortunately there are not enough interested people in any given area who can collect the fauna in the specific places which are to be changed. Most museums, maintaining collections of systematic and geographical value, would be delighted to receive such material for their collections, as the specimens lodged in their cabinets would be the only indication that these species once existed in the area which had been changed.

Pollution is not limited by any means to our freshwater

rivers and lakes. Certainly most of our harbors and estuarine areas are badly polluted, not only from sewage and industrial waste, but from oil spillage and run-off from city streets and highway systems. All intertidal species are affected by the last mentioned source, and at this time there appears to be no relief in sight from this type of pollution. With the continued increase in the number of automobiles and trucks, more and more lost oil will reach our streams and seashores. Pollution of this kind is of direct economic importance as it affects the shell fisheries as well as feeding areas for ducks and shore birds and eventually even inshore fisheries.

Just how much pollution may be affecting our land mollusks is difficult to assess, as there are so many other factors deleterious to their existence. Wide use of pesticides, weed killers and other chemicals must do considerable damage to the molluscan populations in the immediate vicinity where they are used, and where surface run-off exists; this could affect other areas seriously. Many times it is the indirect factor which is the most serious. In the drainage of certain portions of the Everglades in southern Florida it was not the loss of water which directly affected the tree snails of the genus *Liguus* but the fires during the winter months which were encouraged by the dryness of the 'glades.

The pollution and destruction of our natural areas is a local as well as a state and national problem. The development of an area for housing or industry should not mean the almost automatic loss of natural beauty and the destruction of the fauna. In order to improve the situation or even to prevent further destruction, a constant battle must be fought for the preservation of our natural heritage.

Pages i-xvi published November 8, 1965.

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

VOLUME 2 AUGUST 13, 1955 NUMBER 19[1]

The North American Genus Lioplax in the Family Viviparidae[2]

By WILLIAM J. CLENCH AND RUTH D. TURNER

VOLUME 2 SEPTEMBER 22, 1956 NUMBER 20

The Eastern Pacific Marine Mollusks Described by C. B. Adams

By RUTH D. TURNER

VOLUME 2 JANUARY 23, 1957 NUMBER 21

Charles Johnson Maynard and his work in Malacology

By RUTH D. TURNER

VOLUME 2 MAY 29, 1958 NUMBER 22

The Genus Hemitrochus in Puerto Rico

By RUTH D. TURNER[1]

BOOK REVIEW

Voyage aux Iles de Ténériffe, La Trinité, Saint-Thomas, Saint-Croix et Porto Rico by Andre-Pierre LeDru. Published by Arthus Bertrand, Paris 1810. Vol. 1, 47+315 pages; Vol. 2, 324 pages, 1 map. —R. D. TURNER

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

VOLUME 2 APRIL 29, 1959 NUMBER 23

Notes on the Genus Taheitia (Truncatellidae) in New Guinea with the description of a new species

By RUTH D. TURNER

VOLUME 2 OCTOBER 20, 1959 NUMBER 24

Calvin Goodrich; a Bibliography and Catalogue of His Species

By JOSEPH ROSEWATER

VOLUME 2 NOVEMBER 25, 1959 NUMBER 25

A Comparison of *Cyclopecten nanus* Verrill and Bush and *Placopecten magellanicus* (Gmelin)

By ARTHUR S. MERRILL *

VOLUME 2 MAY 3, 1961 NUMBER 26

Land and Freshwater Mollusks of Caicos, Turks, Ragged Islands and Islands on the Cay Sal Bank, Bahamas

By WILLIAM J. CLENCH

BOOK REVIEW

Traité de Zoologie, published under the direction of Pierre-P. Grassé, 1960, Vol. 5, fascicule 2, Embranchement des Mollusques, pp. 1625-2164, text figs. 1469-1830, and 2 colored plates. Masson et Cie Editeurs, Libraires de l'Académie de Médecine, 120 Boulevard Saint-Germain, Paris, France.

—RUTH D. TURNER

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

VOLUME 2 FEBRUARY 26, 1962 NUMBER 27

A Catalogue of the Viviparidae of North America with Notes on the Distribution of Viviparus georgianus *Lea*

By WILLIAM J. CLENCH

VOLUME 2 FEBRUARY 26, 1962 NUMBER 28

***Nettastomella japonica* Yokoyama in North America and notes on the Pholadidae**

By RUTH D. TURNER

VOLUME 2 AUGUST 7, 1964 NUMBER 29

New species of *Tellina* from the Western Atlantic

By KENNETH J. BOSS
U.S. Fish and Wildlife Service
Washington, D.C.

VOLUME 2 AUGUST 7, 1964 NUMBER 30

Anatomy and Relationships of *Temnoconcha brasiliana* Dall

By KENNETH J. BOSS[1] AND VIDA C. KENK[2]

Supplement to the Poison Cone Shell[1]

By WILLIAM J. CLENCH

Occasional Papers On Mollusks

Published by
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Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

VOLUME 2 SEPTEMBER 25, 1964 NUMBER 31

Land and Freshwater Mollusca of the Cayman Islands, West Indies

By WILLIAM J. CLENCH

Remarks on the relationships of the Butterflies (excluding Skippers) of the Cayman Islands

By HARRY K. CLENCH
Carnegie Museum, Pittsburgh, Penna.

Remarks on the relationships of the Reptiles and Amphibians of the Cayman Islands

By ERNEST WILLIAMS
Museum of Comparative Zoology

VOLUME 2 JULY 9, 1965 NUMBER 32

The Genus *Viviparus* (Viviparidae) in North America[1]

By WILLIAM J. CLENCH AND SAMUEL L. H. FULLER[2]

VOLUME 2 NOVEMBER 8, 1965 NUMBER 33

Catalogue of the Family Pandoridae (Mollusca: Bivalvia)

By KENNETH J. BOSS
Ichthyological Laboratory
Bureau of Commercial Fisheries, Fish and Wildlife Service
Department of the Interior, Washington, D.C.

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

VOLUME 2 NOVEMBER 8, 1965 NUMBER 34

Review Number and Index

Supplement to the Catalogue of the Genus Liguus
(*Occasional Papers*, 1: No. 10)
By WILLIAM J. CLENCH

Supplement to the Catalogue of the Family Truncatellidae
(*Occasional Papers*, 1: No. 13)
By WILLIAM J. CLENCH

Supplement to the North American Genus Lioplax
(*Occasional Papers*, 2: No. 19)
By WILLIAM J. CLENCH

Occasional Papers On Mollusks

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VOLUME 3 FEBRUARY 8, 1967 NUMBER 35*

Illustrations of all the Mollusks described by Berlin Hart and Samuel Hart Wright**

By RICHARD I. JOHNSON

* Volume 3 starts with Number 35.
** Supported in part by the William F. Milton Fund, Harvard University.

The Henry G. Frampton Collection of Florida *Liguus*

By WILLIAM J. CLENCH AND KENNETH J. BOSS

VOLUME 3 FEBRUARY 15, 1967 NUMBER 36

William Gaillard Mazÿck (1846-1942) with a Bibliography and Catalogue of his species

By WILLIAM J. CLENCH

BOOK REVIEW

Shell Collecting, An Illustrated History, by S. Peter Dance. Published by the University of California Press, Berkeley and Los Angeles 1966, pp. 1–344, 35 plates, and 31 text figures.
WILLIAM J. CLENCH

VOLUME 3 FEBRUARY 24, 1967 NUMBER 37

Notes on *Pleurobema collina* (Conrad) from the James River, Virginia

By KENNETH J. BOSS AND WILLIAM J. CLENCH

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoology, Harvard University
Cambridge, Massachusetts

VOLUME 3 FEBRUARY 6, 1970 NUMBER 38

Land Mollusca of Saba Island, Lesser Antilles

By WILLIAM J. CLENCH

VOLUME 3 FEBRUARY 6, 1970 NUMBER 39

The Genus *Priotrochatella* (Mollusca: Helicinidae) of the Isle of Pines and Jamaica, West Indies

By WILLIAM J. CLENCH AND MORRIS K. JACOBSON

VOLUME 3 MAY 14, 1971 NUMBER 40

Critical Estimate of the Number of Recent Mollusca

By KENNETH J. BOSS

INTRODUCTION

BOOK REVIEW

Kathleen Yerger Johnstone. 1970. Collecting Seashells. Grosset and Dunlap, 198 pp., 6 colored plates, many figures. $5.95. K. J. Boss

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

VOLUME 3 JUNE 2, 1972 NUMBER 41

ILLUSTRATIONS OF
ALL OF THE MOLLUSKS DESCRIBED
BY LORRAINE SCREVEN FRIERSON

By RICHARD I. JOHNSON

BOOK REVIEWS

STANLEY, STEVEN M. 1970. *Relation of Shell Form to Life Habits of the Bivalvia (Mollusca).* Geological Society of America, Colorado Building, P. O. Box 1719, Boulder, Colorado 80302, Memoir 125, 276 pp., 40 pls., 48 text-figs. $10.00. — K. J. BOSS

HABE, TADASHIGE. 1971. *Shells of Japan.* Translated by T. I. Elliot. Hoikusha Publishing Co., Ltd. 139 pp., 50 colored and black and white plates, many figures. — M. S. BELLE

VOLUME 3 JUNE 2, 1972 NUMBER 42

ON THE TAXONOMY OF
CHAETOPLEURA FULVA (WOOD 1815)
(MOLLUSCA: POLYPLACOPHORA)

By ROBERT C. BULLOCK

BOOK REVIEW

BURGHARDT, GLENN, and LAURA BURGHARDT. 1969. A *Collectors's Guide to West Coast Chitons.* Special Publication No. 4, San Francisco Aquarium Society, 45 pp., 7 figures, 4 colored plates. $4.95. — ROBERT C. BULLOCK

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

VOLUME 3 JUNE 2, 1972 NUMBER 43

THE FRESH-WATER, BRACKISH, AND NON-JAMAICAN LAND MOLLUSKS DESCRIBED BY C. B. ADAMS

By RICHARD I. JOHNSON AND KENNETH J. BOSS

BOOK REVIEWS

ANDREWS, JEAN. 1971. *Sea Shells of the Texas Coast.* University of Texas Press, Austin and London, xvii + 298 pp., numerous figures. $17.50. — ROBERT C. BULLOCK

GRAHAM, ALASTAIR. 1971. *British prosobranch and other operculate gastropod molluscs.* Synopses of the British Fauna, No. 2, New Series. Published for the Linnean Society of London by Academic Press, London and New York, 112 pp., 118 figs. $4.00. — K. J. Boss

VOLUME 3 JUNE 2, 1972 NUMBER 44

NOTES ON THE GENUS CHITON IN THE WESTERN INDIAN OCEAN (MOLLUSCA: POLYPLACOPHORA)

By ROBERT C. BULLOCK

BOOK REVIEW

THORSON, GUNNAR. 1971. *Life in the Sea.* World University Library, McGraw Hill Book Co., New York, Toronto, 256 pp., numerous illustrations. $2.45.
— N. Knowlton

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoology, Harvard University
Cambridge, Massachusetts

VOLUME 3 JUNE 29, 1973 NUMBER 45

MONOGRAPH OF *CERATODISCUS* (ARCHAEOGASTROPODA; HELICINIDAE)

By KENNETH J. BOSS AND MORRIS K. JACOBSON

BOOK REVIEW

CARRASCO FRANCO, GERMÁN. 1971. *Arte Pre-Colombiano de México. Conchas y Caracoles.* Lito Offset Fersa, Av. Central 212, Ciudad de México. 23 pp. text and 48 colored plates. — K. J. Boss

VOLUME 3 JUNE 29, 1973 NUMBER 46

DISTRIBUTION OF HYDROBIIDAE, A FAMILY OF FRESH AND BRACKISH WATER GASTROPODS, IN PENINSULAR FLORIDA

By RICHARD I. JOHNSON

New Records for the Genus Lioplax*

By WILLIAM J. CLENCH

Lioplax sulculosa (*Menke*)

BOOK REVIEW

CLARKE, ARTHUR H. 1973. *The Freshwater molluscs of the Canadian Interior Basin.* Malacologia, 13 (1-2): 1-509. — R. I. JOHNSON

Occasional Papers On Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

VOLUME 3 November 29, 1973 NUMBER 47

THE JAMAICAN LAND SHELLS DESCRIBED BY C. B. ADAMS

MORRIS K. JACOBSON
American Museum of Natural History
New York, New York 10024
and
KENNETH J. BOSS
Museum of Comparative Zoology, Harvard University
Cambridge, Massachusetts 02138

BOOK REVIEW

EVANS, J. G. 1972. *Land Snails in Archaeology. With special reference to the British Isles.* Seminar Press. London and New York. xii + 436 pp., 145 figures, 17 tables. $22.50. — K. J. Boss

NEWS AND ANNOUNCEMENTS

* * * * * * *

SYMPOSIUM ON LITTORINIDAE. — A one-day Symposium on *Taxonomic Trends in the Littorinidae* was held at the Royal Scottish Museum, Edinburgh, on Tuesday, March 19, 1974. The Symposium, the first restricted to this family of the prosobranch Gastropoda, was chaired by Sir Maurice Yonge and attended by 37 people with interests in the Littorinidae. Talks were presented on a range of littorinid topics; probably the most noteworthy contribution was unpublished evidence given by Dr. J. Heller that the polymorphic species *Littorina saxatilis* (Olivi) should be regarded as containing at least 4 separate species.

The meeting unanimously endorsed the suggestion that an informal littorinid group should be formed, with an international membership, as far as possible comprising all workers actively interested in these gastropods. This idea had previously received postal support from over 20 others, mostly from abroad, who were unable to attend the meeting. Anyone wishing to learn more about the group should write to the appointed coordinator, Charles Pettitt, Manchester Museum, The University, Manchester M13 9PL, England.

At the meeting Mr. Pettitt displayed a proof copy of the *Indexed Bibliography of the Family Littorinidae* (*Gastropoda: Mollusca*) 1758-1973 compiled by him and now published by the Manchester Museum (*M. M. Publication N.S.* 4. 74). This bibliography, printed in A4 size with 'plasticised' covers, contains about 730 references to world-wide Littorinidae; there is a subject and a general systematic index, with a special index of new generic and specific descriptions. The price is £0. 75p. but the author has arranged that individual workers and members of recognised conchological societies may order a personal copy at cost price, 50p.; to both prices should be added 8p. postage in U.K., 15p. overseas. Requests should be sent to Charles Pettitt, at the above address; cheques, etc., should be made payable to Manchester Museum.

CHANGE IN EDITORIAL AND BUSINESS OFFICES OF *MALACOLOGIA*. — With the completion of Vols. 12, 13 and 14 for the year 1973 and the retirement of J. B. Burch as Editor-in-Chief, the location of the editorial office of *Malacologia*, International Journal of Malacology, has been transferred to the Academy of Natural Sciences of Philadelphia. The business office was transferred to Philadelphia in 1972. The new editors and directors of *Malacologia* are George M. Davis and Robert Robertson. The journal's various offices were previously located in the Museum of Zoology, The University of Michigan, where the journal had been under the direction of Dr. Burch since its inception. Anne Gismann (Maadi, A. R. Egypt) and C. J. Bayne (Corvallis, Oregon, U.S.A.) will continue to assist with the editorial responsibilities as General Editors. Mrs. Gismann has served in this capacity since the journal began in 1962, and Dr. Bayne since 1970.

The journal will continue to be published and controlled by the Institute of Malacology (incorporated address: 2415 South Circle Drive, Ann Arbor, Michigan 48103, U.S.A.). Drs. Robertson (President), Burch (President-Elect) and Davis (Executive Secretary-Treasurer) are Sponsor Members and Trustees of the Institute of Malacology, along with J F. Allen (Emeritus), C. J. Bayne, E. G. Berry (Emeritus), K. J. Boss, M. R. Carriker (Past President), N. F. Sohl (Past President), C. F. E. Roper, A. G. Smith (Past President) and S. K. Wu.

All correspondence regarding editorial, business and subscription matters should be addressed to *Malacologia*, c/o The Department of Malacology, Academy of Natural Sciences of Philadelphia, 19th and Parkway, Philadelphia, Pennsylvania 19103, U.S.A.

SOCIÉTÉ FRANÇAISE DE MALACOLOGIE. — The Society will hold 2 meetings during 1975. On 7 and 8 March 1975, a symposium on Polymorphism in fossil and Recent molluscs will be held in Dijon (Institut des Sciences de la Terre de l'Université de Dijon, France). The 3rd Congress of the French Malacological Society will meet in La Rochelle (Institut Universitaire et Technique de La Rochelle, France) on 16-22 June 1975. During this Congress an international symposium will be held on Applied marine Malacology.

Authors of communications must be members of the Society. For further information write to Société Française de Malacologie, 55, rue Buffon, 75005 - Paris, France.

BOOK REVIEWS

POLYPLACOPHORA OF THE CARIBBEAN REGION. P. Kaas. Studies on the Fauna of Curaçao and other Caribbean Islands. 1972. Vol. 41, No. 137, 162 p, 9 pls. Martinus Nijhoff, The Hague, The Netherlands.

The chitons of the Caribbean region have at last been examined in some detail, and this extensive publication by Kaas is certainly the result of much effort. Of the 34 known Caribbean species, 32 were examined personally by Kaas, including 5 new species and a new variety. The material available for study was derived primarily from collections of Wagenaar Hummelinck; the Rijksmuseum van Natuurlijke Histoire, Leiden; the Zoologisch Museum, Amsterdam; and a few private collections. During his long study of these chitons, Kaas was able to examine type specimens, or photographs of them, housed in a number of major institutions both in the U.S.A. and Europe.

The monograph begins with an historical review of West Indian chitons, and annotated lists of species record the contributions made by Linnaeus, Chemnitz, Guilding, Reeve, C. B. Adams, Shuttleworth, Rochebrune, Pilsbry and others. The systematic account which follows provides keys to the families, genera and species, and for each species detailed descriptions of shell and girdle morphology are provided. The synonymies presented are abbreviated in form, but include a review of the systematic literature. The numerous drawings and photographs at the end of the text are among the better illustrations to have accompanied papers on polyplacophoran systematics.

Conclusions reached by Kaas are, in some cases, not only interesting but contribute significantly toward our knowledge of West Indian chitons. *Ischnochiton bermudensis* Dall & Bartsch 1911 is noted to be conspecific with *I. boogii* Haddon 1886, a fact overlooked by Leloup (1938, *Bull. Mus. roy. Hist. natur.*, Belg., 14(51): 1-11). The common Caribbean species often referred to as *Ischnochiton* (*Stenoplax*) *limaciformis* (Sowerby) is shown to be specifically distinct from Sowerby's eastern Pacific species, and Kaas uses the earliest valid *nomen* for this species, *I. purpurascens* (C. B. Adams 1845).

Kaas' efforts will no doubt stimulate others to look more critically at West Indian Polyplacophora, for even his studies of some of the most common species are not conclusive. *Acanthochitona balesae* Pilsbry is recognized as a nude name, but Kaas has overlooked the fact that Abbott (1954, *American Seashells*, D. Van Nostrand, New York, p 318) previously validated Pilsbry's name, and *A. elongata* Kaas must be considered a junior synonym of *A. balesae* 'Pilsbry' Abbott. Kaas describes a closely related species from the southern Caribbean, *A. interfissa*; its relationship with *A. balesae* should be investigated.

The new species and comments on previously described ones suffer somewhat from a lack of material available for study. Having a series of specimens of *Ischnochiton erythronotus* available for examination, Kaas concludes (p 86) that it is "one of those variable species of which the extreme forms are different enough to make one believe that they belong to separate species, as long as one has not set eyes upon intermediate forms." But *Lepidochitona rosea* n. sp. is described (p 28) on the basis of 2 specimens "in a bad state when I received them," and is compared with only 6 specimens of *L. liozonis*. Only a single specimen was used in the description (p 44) of *Acanthochitona bonairensis* n. sp., 5 in the description (p 53) of *A. interfissa* n. sp., and 2 in the description (p 89) of *Ischnochiton pseudovirgatus*

n. sp. All of Kaas' new species may, indeed, be new; at least one, *Lepidochitona rosea*, appears to have been described more recently by Righi (1973, *Papéis Avulsos Zool.*, S. Paulo, 26: 268) as *L. montoucheti*. Finally, Kaas recognizes that *Lepidochitona tropica* Pilsbry is a nude name. Since the species was previously named twice (*Ischnochiton liozonis* Dall & Simpson 1901; *Trachydermon parvulus* Leloup 1941), Kaas does not propose an additional name, but because Pilsbry's Florida specimens "may be considered at best a local form or variety," Kaas (p 25) "for safety's sake" introduces *tropica* as a new variety, a name which has no taxonomic validity according to Article 15 of the International Code of Zoological Nomenclature.

It should also be mentioned that Kaas' provincial study has not usually included information on the interesting relationships which no doubt exist between some West Indian species and others from the Panamic faunal province. *Ischnochiton boogii* Haddon is reported from both oceans; Kaas uses the name *boogii*, but simply states (p 76): "Whether specimens from Peru are identical to those from the Caribbean area needs confirmation, however." *Acanthochitona rhodea* (Pilsbry) is treated as a Caribbean species, but no mention is made that it also occurs in the Panamic province (e.g., see Keen, 1971, *Sea Shells of Tropical West America*, 2nd ed. Stanford University Press, Stanford, California, 1064 p), although a reference is noted to Keen's work. More adequately treated is Bergenhayn's record of the occurrence in the Galapagos Islands of the West Indian *Callistochiton shuttleworthianus*, but Kaas states (p 101) that "only the examination and comparison of the actual specimens would justify a decision whether they are identical or not."

Kaas makes little effort to comment on polyplacophoran phylogeny; his use of generic and familial taxa must be considered conservative. *Chaetopleura*, *Callistochiton* and *Ischnochiton*, for instance, are all considered to belong to the Ischnochitonidae. All "*Ischnochiton*" species are placed in the genus *Ischnochiton*, a sharp contrast to the work of Thorpe (*in*: Keen, 1971, *op. cit.*). Kaas briefly mentions Thiele's classification (p 66) but states that it is not satisfactory, "as it does not contribute to a better understanding of the true relationships of the numerous *Ischnochiton* species." Kaas does not elucidate, and future problems, such as the use of the names *Stenoplax* and *Radsiella*, remain for others to examine.

Kaas' work on West Indian chitons has given malacologists a strong base which, hopefully, will encourage systematists and ecologists to be more aware of these interesting and at times abundant animals. It now should be much easier to identify most of the Caribbean species, a task not done readily in the past, even by competent malacologists. Kaas is to be commended for this large work, and it is hoped that he will continue his investigations on polyplacophoran systematics.

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FLUKES AND SNAILS. C. A. Wright. Hafner Press Division of Macmillan Co., Inc., 866 3rd Avenue, New York, N. Y. 10022, U.S.A. August 1973. 168 p, 15 figs., 16 pls. US$ 7.50.

The rapid development of parasitology from a general study of systematics and physiology to a discipline with a more ecological approach created the need for an informative book such as *Flukes and Snails*. Its emphasis on ecological aspects of the intramolluscan stages of various non-human digenetic trematodes, as depicted by the author, produces a refreshing change from many of the more classical studies that deal only with adult worms in man. This innovation interests not only the newer and established helminthologists and malacologists, but should appeal to all invertebrate zoologists.

The book covers 5 main areas: general biology and relationships of Digenea (Chapter 1), the Mollusca (Chapter 2), development of life cycles, behavior and ecology of flukes in molluscan hosts (Chapters 3-5), host-parasite relationships (Chapter 6) and taxonomy and taxonomic problems (Chapter 7). The first area, the chapter on "Flukes," traces the historical setting of the Digenea in the phylum Platyhelminthes and other closely related phyla. Also discussed in Chapter 1 are the origin of flukes and theories concerning reproduction of trematodes in their molluscan hosts. The 2nd chapter, titled "Molluscs," deals with the origins and affinities of the 6 living classes of molluscs as set forth by a parasitologist, and the chapter has some information on the skin of mollusks, their mantle and subdermal tissues, and on the vascular, digestive, reproductive and endocrine systems. The 3rd area (Chapters 3-5) considers the development and behavior of larval digenetic trematodes in the first intermediate (molluscan) host. Chapter 3 deals with the life cycle from egg production to the time when the miracidia actively or passively enter snails. Development of miracidia in subsequent stages of the cycle is considered in Chapter 4. This 3rd area is concluded with ecological considerations of schistosomiasis, fascioliasis, paragonimiasis and clonorchiasis (Chapter 5).

The delicate balances that exist in the digenetic trematode-mollusc system are considered under "Physiological host-parasite relationships and pathology" (Chapter 6). The parasites' intramolluscan life cycle stages must be successfully completed before the snail host dies. Interference in the distribution and reproduction of the host by the fluke would jeopardize its own survival. This section also deals with susceptibility of the snail host; the infectivity and compatibility of both snails and parasite. There are a wide range of topics considered, such as general pathology, gigantism, parasitic castration, immunity, concurrent infections, interspecific competition among flukes, as well as the pressure by the parasite on molluscan populations.

In Chapter 7, the author discusses many taxonomic problems associated with both the digenetic trematodes and their snail hosts. Modern techniques, such as chromatography, electrophoresis, immunology and others, may serve more clearly to define the trematode and snail species, as well as to indicate their interrelationships.

This book is very useful in providing valuable information dealing with the interphase of digenetic trematodes and their molluscan hosts. It is unfortunate that references to some basic studies from other countries are omitted; better references are needed, as between the figures and plates to the text. Also, there is too little emphasis on molluscs.

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MALACOLOGICAL CALENDAR

The malacological calendar printed below serves to give at a glance the dates of coming malacological events. Further details of the various functions may be obtained from society or program officers. Information regarding forthcoming malacological meetings, seminars, symposia, congresses, etc., are welcome and should be sent to the editorial office of *Malacological Review*, addressed to P. O. Box 801, Whitmore Lake, Michigan 48189, U.S.A.

1974

August

3-8 — Fortieth Annual Meeting of the American Malacological Union, Springfield, Massachusetts, U.S.A. Hosts will be the Springfield Museum of Science and the Connecticut Valley Shell Club. Address inquiries to Mr. Earl B. Reed, Springfield Science Museum, 236 State Street, Springfield, Massachusetts 01103, U.S.A.

17-Sept. 7 — Third Australian Shell Convention, Perth, Australia. Sponsored by the Malacological Society of Australia and the Western Australian Shell Club. 19-24 August - shell excursions; 26-31 August - presentation of lectures and papers; 2-7 September - shell excusions. Address inquiries to Mr. B. Hargreaves, Secretary, 56 Wroxton St., Midland, Western Australia 6056.

September

2-8 — Fifth European Congress of Malacology and Symposium, sponsored by the Unitas Malacologica Europaea, to be held in Milan, Italy, at the Civic Museum of Natural History and at the Hydrobiological Station and Aquarium of the Municipality of Milan. Address inquiries to Fifth European Congress of Malacology, Civic Museum of Natural History, Corso Venezia 55, Milan, Italy.

October

19 — Conchological Society of Great Britain and Ireland. Lecture by M. J. Bishop, "West American marine molluscs - some micro-habitats." Exhibition of American marine mollusks. Location: The Conversazione Room, British Museum (Natural History), London. Time: 2:30 p.m.

November

16 — Conchological Society of Great Britain and Ireland. Lecture by A. J. Cain, "Natural selection in *Cepaea*." Exhibition of British land Mollusca. Location and time: same as October meeting.

December

14 — Conchological Society of Great Britain and Ireland. Lecture by J. F. Peake, "Research on ponds." Exhibition of freshwater mollusks. Location and time: same as October meeting.

1975

January

18 — Conchological Society of Great Britain and Ireland. Lecture by E. E. Sandor, "The cultured pearl." Exhibition of pearls, oysters and mussels. Location and time: same as October meeting.

Malacological Review, 1974, 7: 167-191

CONTENTS OF CURRENT SERIAL PUBLICATIONS ON MOLLUSKS

The contents of current malacological serial publications, as shown by their tables of contents, are herewith reproduced as a service to the scientific community. The publications are listed in alphabetical order. Also listed are the locations of the editorial offices. Those publications that do not have their contents printed in this current issue of *Malacological Review* (Vol. 7, No. 2) are marked by an asterisk in the right hand column below; contents of these publications will be included in future issues of *Malacological Review.*

Journal	Location of Editorial Office	Page
The American Malacological Union, Inc., Bulletin	Ottawa, Canada	*
Archiv für Molluskenkunde	Frankfurt-am-Main, Germany (FR)	168
Argamon	Jerusalem, Israel	*
Basteria	Leiden, The Netherlands	169
Comunicaciones de la Sociedad Malacológica del Uruguay	Montevideo, Uruguay	*
Conchiglie	Milano, Italy	170
The Echo	San Francisco, Calif., U.S.A.	*
Gastropodia	Fleetwood, Pa., U.S.A.	171
Haliotis	Paris, France	*
Johnsonia	Cambridge, Mass., U.S.A.	*
Journal de Conchyliologie	Mosman, N.S.W., Australia	*
Journal of Conchology	Bromborough, Cheshire, U.K.	*
Journal of the Malacological Society of Australia	Geelong, Vict., Australia	172
Lavori della Società Malacologica Italiana	Milano, Italy	*
Malacologia	Ann Arbor, Mich., U.S.A.**	*
Malacological Review	Whitmore Lake, Mich., U.S.A.	173
Malakologische Abhandlungen	Dresden, Germany (DR)	*
The Nautilus	Greenville, Dela., U.S.A.	175
Occasional Papers on Mollusks	Cambridge, Mass., U.S.A.	137
Proceedings of the Malacological Society of London	Reading, U.K.	177
Proceedings of the National Shellfisheries Association	Oxford, Md., U.S.A.	*
Soosiana	Baja, Hungary	178
Sterkiana	Columbus, Ohio, U.S.A.	183
The Veliger	Berkeley, Calif., U.S.A.	184
Venus	Tokyo, Japan	186

**To change to Philadelphia, Pa., U.S.A., beginning with Vol. 15, 1974.

Archiv für Molluskenkunde

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Band 103 Nummer 4/6

Inhalt.

Schlickum, W. R. & Strauch, F.: Die neogene Gastropoden-Gattung *Mesodontopsis* Pilsbry 1895. 153

Loosjes, F. E. & Loosjes-van Bemmel, A. C. W.: Das System der Clausiliiden (Gastropoda: Euthyneura). 175

Nordsieck, H.: Zur Anatomie und Systematik der Clausilien, XIII. Neue Balkan-Formen der Mentissoideinae und Baleinae (mit taxonomischer Revision der zugehörigen Gruppen). (Tafel 6-7, 7a). 179

Falkner, G.: Studien über *Trichia* Hartmann, I. *Trichia (Trichia) graminicola* n. sp. aus Südbaden (Gastropoda: Helicidae). 209

Reischütz, P. L.: *Arion (Microarion) obesoductus* n. sp., eine neue Nacktschnecke aus Niederösterreich. 229

Girod, A., Bona, E. & Mariani, M.: Zwei neue Fundorte von *Marstoniopsis insubrica* (Küster) südlich der Alpen. 231

Walter, J.: Vergleichende Untersuchung von *Lymnaea auricularia* und *Lymnaea ovata* (Gastropoda: Basommatophora) mittels Chromatogrammen des Körperschleims. 235

Schlickum, W. R. & Moayedpour, E.: Zur miozänen Gastropodenfauna der Rhön. 239

Götting, K.-J.: Die Polyplacophora der karibischen Küste Kolumbiens. (Tafel 8-11). 243

Zilch, A.: Die Typen und Typoide des Natur-Museums Senckenberg, 52: Mollusca: Hydrocenidae. (Tafel 12-13). 263

Zilch, A.: Die Typen und Typoide des Natur-Museums Senckenberg, 53: Mollusca: Truncatellidae. (Tafel 14-15). 273

Frankfurt am Main 1973

Arch. Moll. | 103 | (4/6) | 153—282 | Frankfurt a. M., 30. 11. 1973

BASTERIA

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NEDERLANDSE MALACOLOGISCHE VERENIGING

Vol. 37, No. 1–2, pp. 1–50

10–V–1973

INHOUD

W.J. KUIJPER: De zoetwatermollusken van het duingebied ten noorden van Den Haag 1
S. VAN DER SPOEL: Hyalea orbignii Rang, 1827: a fossil Cavolinia species (Mollusca, Pteropoda) 21
C. O. VAN REGTEREN ALTENA: Notes sur les limaces, 19. Description d'une nouvelle espèce du genre Deroceras de la France 25
A. STIVA: Cernuella neglecta (Drap.), een nieuwe soort voor België 29
H. SCHUETT: Einige Süsswassermollusken der zentralen Hochtäler Westasiens 31
H.K. MIENIS: Notes on recent and fossil Neritidae 3. Neritina juttingae, new name for Nerita aculeata Gmelin, 1791, non Müller, 1774 (Mollusca, Gastropoda) 39
G.R. FOSTER: Soil type and habitat of the aquatic snail Lymnaea (Galba) bulimoides Lea during the dry season 41
Boekbespreking: Nordsieck 47
Book review: Green & Hill 49

LEIDEN

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Anno IX - n. 7-8 luglio-agosto 1973

SOMMARIO

FRANCHINI D. A. - Il genere *Typhis* MONTFORT, 1810 nel Mar Mediterraneo . . . . . pag. 125

CAPROTTI E. - Sul trend evolutivo di alcune specie del genere *Amyclina* IREDALE, 1918 del Neogene del Nord Italia 143

GHISOTTI F. - Glossario - I colori delle conchiglie e le loro denominazioni latine . . . 153

FRANCHINI D. A. - Recensioni bibliografiche . . . 158

* * * *

Anno IX - n. 9-10 settembre-ottobre 1973

SOMMARIO

CAPROTTI E. - Il genere *Ficus* (BOLTEN) ROEDING, 1798 nel Pliocene mediterraneo . . pag. 161

CESARI P. - Le specie mediterranee d'acqua salmastra della fam. Ellobiidae . » 181

RINALDI E. - Presenza di bisso in *Scapharca* cfr. *cornea* (REEVE) . . . . . » 211

MALDONADO QUILES A. - Segnalazione di due molluschi nuovi per il Mediterraneo . . . » 213

GHISOTTI F. - Recensioni bibliografiche . . . » 216

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CONTRIBUTIONS

The Sexual Evolution of the Polygyrid Snails: *Pulmonata, Stylommatophora*. . . . . . *85-90.*

Part 2: *Pulmonata, Camaenidae:* Comparative Sexology and Genital Development of *Caracolus carocolla* (L.), *C. marginella* (Gmelin), and *Polydontes lima* (Ferussac). . . . . *90-95, Pls. 38-41.*

***Ashmunella carlsbadensis* Pilsbry Living in Carlsbad Caverns National Park**. . . . . *95-96, Pl. 41.*

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JOURNAL OF THE MALACOLOGICAL SOCIETY OF AUSTRALIA

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VOLUME 2 NUMBER 4 31 MARCH 1973

CONTENTS

G. P. WHITLEY and W. F. PONDER. Obituary. Tom Iredale. (1880-1972) 361

T. G. DIX. Histology of the mantle and pearl sac of the pearl oyster *Pinctada maxima* 365

A. SOLEM. *Craterodiscus* McMichael, 1959, a camaenid land shell from Queensland 377

H. M. LAWS. B. C. Cotton: Additions to the index of his new scientific names 387

H. M. LAWS. The chromosomes of *Succinea australis* (Férrusac) 389

P. DINAMANI. Note on a thaisid gastropod with an abnormal tentacle 393

W. F. PONDER and B. R. WILSON. A new species of *Pterynotus* from Western Australia 395

W. F. PONDER. A review of the Australian species of *Penion* Fischer 401

B. J. SMITH. A new species of snail from Lake Pedder, Tasmania, possibly belonging to the family of Valvatidae 429

Title page, Contents of Volume 2, Index of new taxa.

MALACOLOGICAL REVIEW

VOLUME 7, Number 1 1974

CONTENTS

Research Articles

Note sur la répartition en Belgique de trois mollusques Gastéropodes terrestres peu connus: *Acme inchoata* (Prosobranches, Acmidae), *Abida frumentum* (Stylommatophores, Vertiginidae) et *Alexia denticulata* (Basommatophores, Ellobiidae). S. SEVO 1
Electrophoretic studies on foot muscle esterases of some African *Biomphalaria* species. F. M. A. UKOLI 15
Immunological relationships of two species of Lymnaeidae (Mollusca: Basommatophora) from Macedonia, Yugoslavia. J. B. BURCH and S. HADŽIŠČE 25

Brief Communications

A review of some land snails of the eastern United States. L. HUBRICHT 33
Oviposition in the land snail *Anguispira alternata* (Stylommatophora: Endodontidae). A. TOMPA 35
A colchicine hypotonic squash technique for chromosome spreads of pulmonate land snails. N. BABRAKZAI and W. B. MILLER 37

Proceedings and Abstracts, Mollusk Seminar, Ann Arbor, 1973

Program 40
Systematics, Variation and Zoogeography 41
Anatomical systematics of freshwater mussels. W. H. HEARD 41
Comparative reproduction in viviparid snails. V. A. VAIL 42
Studies on Physidae (Pulmonata: Basommatophora). I. Penial complex morphological groupings. G. A. TE 43
Scanning electron microscope studies of the embryonic shell surface sculpture in *Bulinus*. C. M. PATTERSON 45
Freshwater mollusks of Lake Ohrid, Macedonia. S. HADŽIŠČE, J. B. BURCH and C. M. PATTERSON 47
Growth, Development, Behavior, Physiology and Biochemistry 48
Life table parameters of an experimental population of *Omalonyx felina* (Pulmonata: Succineidae). A. L. SHRADER 48
The structure, ciliation and function of the lips of bivalves. T. H. J. GILMOUR 48
The structure of calcareous snail eggs. A. TOMPA 49
Behavioral and physiological studies on locomotion in the giant garden slug, *Limax maximus*. D. J. PRIOR and A. GELPERIN 50
Comparative aspects of the morphology and physiology of a single identifiable neuron in *Helix aspersa*, *Limax maximus* and *Ariolimax californica*. D. SENSEMAN and A. GELPERIN 51
The histochemical identification of galactogen in the Succineidae. P. H. RUDOLPH 52
Organ culture of *Helix pomatia* albumen gland in a defined medium. E. M. GOUDSMIT and S. L. FELDMAN 53

MALACOLOGICAL REVIEW

CONTENTS (continued)

Snails as Intermediate Hosts of Parasites 54
A simple biochemical method for discerning between diploid and polyploid species of the *Bulinus* (*Isidora*) complex. G. K. LINDSAY 54
The genus *Bulinus* and schistosomiasis in North Africa. P. T. LoVERDE 54
Biology and control of *Bulinus truncatus* in Egypt. E. S. DEMIAN and E. G. KAMEL 55
Experimental infection of *Bulinus sericinus* with *Schistosoma haematobium*. S.-K. WU and J. B. BURCH 56
The larval interaction of *Paragonimus ohirai* and *Schistosoma japonicum* in *Oncomelania*. P. T. LoVERDE and M. PARKER. 57

News and Announcements

Meeting of the Institute of Malacology 58
The Conchological Society of Great Britain and Ireland, Program of Meetings for 1974. 59
Deutschen Malakozoologischen Gesellschaft 59
Western Society of Malacologists. 60
American Malacological Union 60
Unitas Malacologica Europaea 60
Lerner Marine Laboratory 60
Voucher Specimens 60
Index Animalium 61
EPA Mollusk Identification Manuals 61
Court case to halt construction on dams on the Duck River, Tennessee 62
Mollusk Seminar, Ann Arbor, Michigan 62

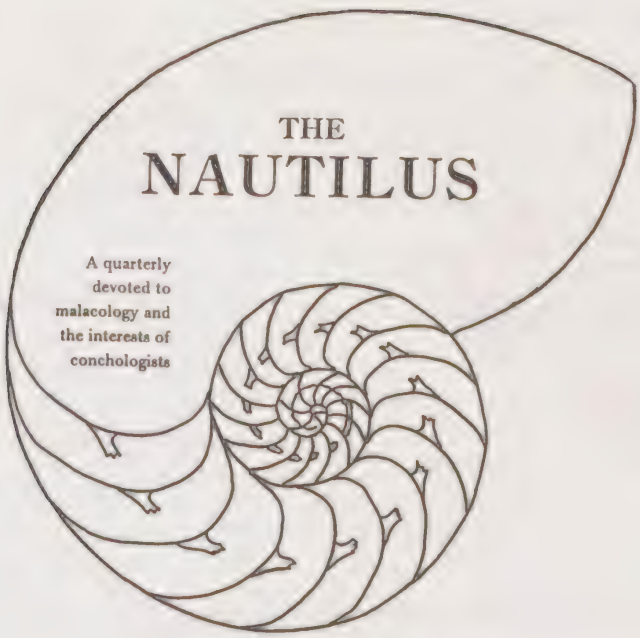
Obituary

George Paul Kanakoff 63

Contents of Current Malacological Periodicals 65
Author index for malacological periodicals. 93

Publications. 101

MALACOLOGICAL REVIEW, P.O.Box 801, Whitmore Lake, Michigan 48189, U.S.A.



THE
NAUTILUS

Volume 87, number 4 – October 1973

CONTENTS

R. Tucker Abbott
Acteon eloiseae, a New Opisthobranch from Arabia 91

Michael A. Rex and Kenneth J. Boss
Systematics and Distribution of the Deep-sea Gastropod, *Epitonium (Eccliseogyra) nitidum* 93

Francisco J. Palacio
On the Double Hectocotylization of Octopods 99

William A. Sodeman, Jr.
The Influence of Light on *Biomphalaria glabrata* 103

Morris K. Jacobson
On the Identity of *Helicina granulum* Pfeiffer (Prosobranchia) 107

Wayne D. Cable
The Valvular Membrane in Young Mactrid Clams, *Spisula solidissima* 110

Kenneth W. Turgeon and Richard A. Fralick
Size and Sex Ratio Differences in *Urosalpinx cinerea* (Say) (Muricidae) from Great Bay, New Hampshire 112

Willard N. Harman
The Mollusca of Canadarago Lake and a New Record for *Lasmigona compressa* (Lea) 114

Richard W. Fullington
Obituary of Elmer P. Cheatum (1901-1973) 115

Book Reviews
(of) Percy A. Morris, 102; Edwin A. Joyce, Jr. 114

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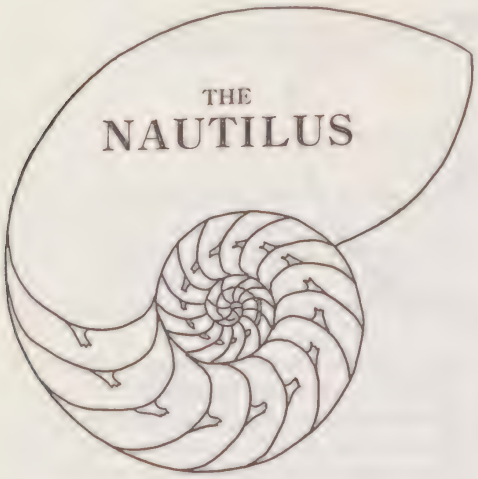

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THE
NAUTILUS

Volume 88, number 1 — January 1974

CONTENTS

Kenneth D. Rose

The Religious Use of *Turbinella pyrum* (Linnaeus), the Indian Chank 1

Lowell L. Getz

Species Diversity of Terrestrial Snails in the Great Smoky Mountains 6

Hal Lewis

A New Species of Hawaiian *Gyrineum* (Cymatiidae) 10

Richard Houbrick

Growth Studies on the Genus *Cerithium* (Gastropoda: Prosobranchia) with Notes on Ecology and Microhabitats 14

Morris K. Jacobson and William E. Old, Jr.

On a Sinistral Specimen of *Liguus virgineus* (with Additional Remarks on the Genus *Liguus)* 28

Edward M. Stern

The Chromosome Number of *Euglandina rosea* (Stylommatophora: Oleacinidae) 29

Book Reviews

(of) American Malacologists, 27; A. Gordon Melvin, 30; Publications Received ii

INDEX TO THE NAUTILUS

An index to The Nautilus, both author and subject matter, will appear every five years. The first index to cover the new format will be issued separately at the completion of volume 90 in early 1977. It will cover volumes 86 through 90 (1972-76). An accumulative index is tentatively planned in 1986 to cover volumes 61 through 100.

PROCEEDINGS OF THE

Malacological Society

OF LONDON

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VOLUME 40 · PART 6 · DECEMBER 1973

CONTENTS

R. H. NISBET. The role of the buccal mass in the trochid 435

S. KANJILAL and C.S.P. SINGH. A new nuculanid genus from the Callovian of Kutch (Gujarat), India 469

B. MERDSOY and J. FARLEY. Phasic activity in the digestive gland cells of the marine prosobranch gastropod, *Littorina littorea* (L.) 473

P. CALOW. Field observations and laboratory experiments on the general food requirements of two species of freshwater snail, *Planorbis contortus* (Linn.) and *Ancylus fluviatilis* (Müll.) 483

H. H. CROWELL. Laboratory study of calcium requirements of the brown garden snail, *Helix aspersa* Müller 491

DEBORAH HEMBROW. Observations on the structure and function of the buccal mass of *Planorbarius corneus* (L.) 505

PAUL H. HARVEY. The distribution of three species of helicid snail in East Yorkshire. I. General survey 523

CHARLES PETTITT. A proposed new method of scoring the colour morphs of *Littorina saxatilis* (Olivi, 1792) (Gastropoda: Prosobranchia) 531

Annual Report of the Council, 1972 – 73 539

Review 540

Index to Volume 40 543

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soosiana

A TUDOMÁNYOS ISMERETTERJESZTŐ TÁRSULAT BÁCS-KISKUN MEGYEI SZERVEZETE BIOLOGIAI SZAKOSZTÁLYÁNAK IDŐSZAKOS MALAKOLOGIAI KÖZLEMÉNYEI

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B E K Ö S Z Ö N T Ő

A magyar malakologusoknak régi vágya teljesül, amikor önálló időszakos kiadvánnyal jelentkezhetnek és számolhatnak be munkásságukról.

Ezt a TIT Bács-Kiskun Megyei Szervezete Biologiai Szakosztályának áldozatkészsége tette most lehetővé. Első szavunk tehát a köszönet. Jelentős lépés ez a kiadvány, mert eddig sok tanulmány - közlési lehetőség hiányában - meg sem iródhatott, ha pedig mégis,esetleg évekig várhatott itthon vagy külföldi folyóiratban a megjelenésre. S ami még ennél is fontosabb: fiatal és kezdő kutatóinkat még biztatni sem tudtuk arra,hogy első mondanivalójukat foglalják irásba.

"Soosiana" áll a cimlapunkon.Tiszteletadás ez és állandó megemlékezés a magyar csigászok Nagy Öregjéről, dr.Soós-ról, aki alig egy éve távozott el közülünk. Hosszu élete és munkássága során sokunknak volt mestere és valamennyiünk tisztelete s ragaszkodása övezte. Ha nem irta volna meg alapvető magyar csigafaunisztikai müveit,akkor előről kellene most kezdenünk a munkát,igy azonban van mire épitenünk. Nevét világszerte ismerik és becsülik,ezért is választottuk azt / a róla elnevezett csigafaj alakjában/kiadványunk ciméül.

Mit akarunk? Számbavenni önmagunkat,megismerni egymás munkáját és eddigi eredményeit,összehangolni a jövő terveit.Rögziteni a magyarországi csigakutatás jelenlegi képét,felvázolni s egyre inkább eltüntetni a térképről a még fel nem kutatott "fehér foltokat".A malakologiát a legtágabb értelemben kivánjuk müvelni: bár tudjuk,hogy a faunisztika az alap,melyre minden további kutatás épülhet,kiadványunkban a tudomány minden ágának helyt kivánunk adni,ha összefüggésben van a malakologiával. S külön is hangsulyozzuk: nem csupán a recens, szárazföldi és édesvizi,hanem a fossilis és tengeri faunáról szóló tanulmányokat is szivesen látjuk.

Ismertetni akarjuk mindazon magyar kutatók munkásságát is, akik már nem élnek köztünk,de azokét a külföldi kutatókét is, akik hazánk puhatestüivel foglalkoztak. A mai külföldi irodalomról pedig - amennyiben a magyar faunát érinti - szintén igyekszünk minél frissebben beszámolni.

Cikkeinket külföldnek is szánjuk, ezért a magyaron kivül legalább még egy idegen nyelven is bő kivonatot adunk róluk, ill.idegen nyelvü cikkeket is közlünk magyar kivonattal.

Tudjuk,hogy ez a terv igen bő, de reméljük, hogy lépésről-lépésre meg is valósithatjuk.Tekintse minden magyar csigász sajátjának is ezt a kiadványt s ne csupán olvassa,hanem irja is.

Köszöntjük tehát olvasóinkat, itt és a külföldön, de egyuttal mindazokat a kutatótársakat és mindenkit,akit munkásságunk érdekel.

Dr.Pintér István

/Keszthely/

Z U M G E L E I T

Ein alter Wunsch der ungarischen Malakologen wird - dank der TIT Organisation des Komitates Bács-Kiskun - mit der Erscheinung der "Soosiana" erfüllt.

Mit dem Titel "Soosiana" wollen wir des Old Great Man der ungarischen Malakologie, Dr.Lajos Soós gedenken, der vor einem Jahr hingeschieden ist und der auch unter den ausländischen Wisserschaftlern überall bekannt war.

Was ist das Ziel dieser Zeitschrift?

Wir möchten die in- und ausländischen Forscher, und alle, die sich dafür interessieren, mit der Tätigkeit, mit den Forschungsarbeiten und Erfolgen der ungarischen Malakologen bekanntmachen. Mit Aufmerksamkeit werden wir die Mitteilungen auch der ausländischen Malakologen verfolgen,insofern sie Ungarns Malakofauna betreffen. "Soosiana" will sich mit dem ganzen Gebiet der Malakologie befassen, also mit der rezenten und fossilen Fauna, mit den Land-,Süsswasser- und auch Meeresmollusken.

Wir hoffen, dieses Vorhaben wird Schritt für Schritt realisierbar sein, und wir bitten dazu um die Mitwirkung aller Malakologen.

Dr.István Pintér

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A Vertigo O.F.Müller 1774 genus magyarországi fajai
/Mollusca,Gastropoda/

irta: Szigethy Anna

A viztelenedés hatása a mocsárerdők és liget-
erdők vizi puhatestűire

The effect of drainage on the water mollusks of
the marsh and gallery forests

irta : Bába Károly

Ásotthalom csigafaunája

Die Schneckenfauna von Asotthalom

irta: Vásárhelyi István

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STERKIANA

NO. 50, JUNE, 1973 COLUMBUS, OHIO JUNE, 1973

HENRY VAN DER SCHALIE AND ELMER G. BERRY

THE EFFECTS OF TEMPERATURE ON GROWTH AND REPRODUCTION OF AQUATIC SNAILS

NO. 51 COLUMBUS, OHIO SEPTEMBER 1973

CLAYDON C. COURI. A NEW PLEISTOCENE FAUNULE FROM MEADE COUNTY, KANSAS. 1

AURÈLE LA ROCQUE. PSEUDOGASTROPODS 10

ANNOUNCEMENTS 10

LYLE F. CHICHESTER AND LOWELL L. GETZ. THE TERRESTRIAL SLUGS OF NORTH-EASTERN NORTH AMERICA 11

REPRINTS OF RARE PAPERS ON MOLLUSCA: LEFEVRE AND CURTIS: STUDIES ON THE REPRODUCTION AND ARTIFICIAL PROPAGATION OF FRESH WATER MUSSELS (CONTINUED FROM NO. 49) . . . . . after page 42

NO. 52 COLUMBUS, OHIO DECEMBER 1973

MARK J. CAMP. PLEISTOCENE LACUSTRINE DEPOSITS AND MOLLUSCAN PALEONTOLOGY OF WESTERN OHIO, EASTERN INDIANA AND SOUTHERN MICHIGAN 1

BRANLEY A. BRANSON. THE RECENT GASTROPODA OF OKLAHOMA, PART VII. THE ZONITIDAE 28

HENRY VAN DER SCHALIE. THE MOLLUSKS OF THE DUCK RIVER DRAINAGE IN CENTRAL TENNESSEE 45

AURÈLE LA ROCQUE. CLAUDE W. HIBBARD (1905-1973) 56

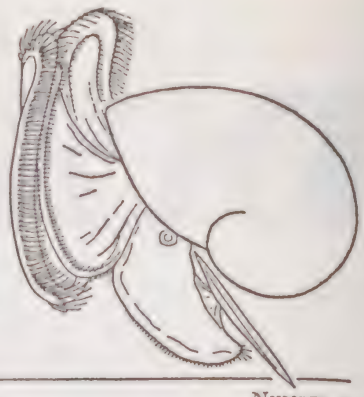
NO. 53 COLUMBUS, OHIO MARCH, 1974

MORRIS K. JACOBSON -- CHARLES WRIGHT (1811-1885) IN CUBA AS REVEALED BY HIS LETTERS 1

YUNG-SAN LIANG -- CULTIVATION OF *BULINUS (PHYSOPSIS) GLOBOSUS* (MORELET) AND *BIOMPHALARIA PFEIFFERI PFEIFFERI* (Krauss), SNAIL HOSTS OF SCHISTOSOMIASIS 7

(To be continued in Sterkiana No. 54)

THE VELIGER



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VOLUME 16 APRIL 1, 1974 NUMBER 4

CONTENTS

Four New Species of Nudibranchs from Tropical West America. (7 Plates)
HANS BERTSCH & ANTONIO J. FERREIRA 343

Recognition and Distribution of *Mytilus condoni* Dall, a Unique Pliocene and Pleistocene Bivalve from the Pacific Coast. (1 Plate)
WARREN O. ADDICOTT 354

On the Affinities of *Humboldtiana fullingtoni* Cheatum, 1972 (Mollusca : Pulmonata : Helminthoglyptidae). (2 Plates; 1 Table; 2 Text figures)
ALAN SOLEM 359

New Occurrences of *Ischnochiton retiporosus* Carpenter, 1864 in the Eastern Pacific Ocean.
BARRY S. KUES 366

On the Absence of Cuttlefish in the Western Atlantic.
GILBERT L. VOSS 367

A Phenology of the Smaller Dendronotacean, Arminacean and Aeolidacean Nudibranchs at Asilomar State Beach Over a Twenty-Seven Month Period. (1 Text figure)
JAMES NYBAKKEN 370

A Late Pleistocene Terrace Faunule from Near La Jolla, California. (1 Plate)
P. F. KARROW & WILLIAM K. EMERSON 374

The West American Hipponicidae and the Application of *Malluvium, Antisabia,* and *Hipponix* as Generic Names. (4 Plates)
I. MCTAGGART COWAN 377

Five New Species of Ovulidae from the Western Pacific (Mollusca : Gastropoda) (1 Plate)
CRAWFORD NEILL CATE 381

The Introduced Semelid Bivalve *Theora (Endopleura) lubrica* in Bays of Southern California. (2 Text figures)
ROGER R. SEAPY 385

[Continued on Inside Front Cover]

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

Second Class Postage Paid at Berkeley, California

CONTENTS — *Continued*

Vertical Intertidal Distribution of *Mytilus edulis*. (3 Text figures)
JUNE R. P. ROSS & DAN GOODMAN 388

A Method for Estimating Live Weight and Body Length from the Shell of *Aplysia willcoxi* Heilprin, 1886. (2 Text figures)
JANET M. KRAKAUER 396

Spawning, Development and Growth in the Pulmonate Limpets *Siphonaria pectinata* Linnaeus, 1758, and *Siphonaria alternata* Say, 1822. (3 Text figures)
JAMES A. ZISCHKE 399

The Food and Feeding Habits of the Cuttlefish *Sepiella inermis* (Férussac & d'Orbigny).
ISABEL TANG & HONG-WOO KHOO 405

Some Notes on the Distribution and Taxonomy of Haliotids (Mollusca : Gastropoda)
ROBERT R. TALMADGE 411

Epicaridium Larvae in *Mytilus californianus* (Mollusca, Bivalvia). (2 Text figures)
NICOLAS K. TEMNIKOW 413

Effects of Body Weight on Feeding Rate and Radula Size in the Freshwater Snail *Pila globosa*.
M. A. HANIFFA & T. J. PANDIAN 415

On the Possible Significance of Enhanced Glutamate Dehydrogenase Activity in Normal and Aestivated *Pila globosa*. (3 Text figures)
CH. RADHA KRISHNA MURTHY, T. PAVAN KUMAR, K. S. BABU & KARUMURI. S. SWAMI 419

NOTES & NEWS 423
Soviet Contributions to Malacology in 1972. MORRIS K. JACOBSON & KENNETH J. BOSS
Re *Laura* Trinchese, 1872 (Gastropoda : Opisthobranchia). A. MYRA KEEN
Geographic Displacement as a Non-Range-Extension of *Tegula gallina* (Forbes) (Gastropoda : Trochidae). JAMES T. CARLTON, ARMAND M. KURIS & MICHAEL S. BRODY
Two Symbioses of *Conus* (Mollusca, Gastropoda) with Brachyuran Crabs. (2 Text figures) FAY HENRY WOLFSON

INFORMATION DESK 433
Differentiation: The Meaning of ICZN Article 13 (a) (i)
R. V. MELVILLE

BOOKS, PERIODICALS & PAMPHLETS 434

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貝類学雑誌
VENUS
THE JAPANESE JOURNAL OF MALACOLOGY

第31巻 第4号 Vol. 31, No. 4

Contents

A New Epitoniid Species from Japan (Text-figs. 1~2) ····· Prince Masahito & Tadashige HABE···(135)

New Calliostomid Species from off Torishima, 580 km South of Tokyo, Japan (Text-figs. 1~2) ·····Kazuo SASAO and Tadashige HABE···(137)

Tutufa tenuigranosa (SMITH) and *T. oyamai*, sp. nov., Hitherto Erroneously Referred to the Former (Text-figs. 1~2)·····Tadashige HABE···(139)

Description of a New Species of the Genus *Otesiopsis* HABE from Mt. Kammuriyama, Fukui Pref., Japan (Gastropoda, Helicarionidae) (Text-figs. 1~5) ·····Masao AZUMA···(143)

Predators on the Benthic Bivalves in Muddy Bottom of the Inland Sea of Japan-I. The Effect of the Predation of *Neverita reiniana* on *Veremolpa micra* (Text-figs. 1~9; Table 1) ·····Hiroshi MUKAI···(147)

Short Note

Halcampella maxima HERTWIG, Host of *Nipponomontacuta actinariophila* YAMAMOTO & HABE (Text-fig. 1) ····· Tadashige HABE···(157)

Spawning in *Telescopium telescopium* (LINNAEUS) (Potamididae—Gastropoda) (Text-figs. 1~2)·····K. RAMAMOORTHI and R. NATARAJAN···(158)

Review & Abstract

The Sea Shells of Sagami Bay edited by Biological Laboratory, Imperial Household·····Iwao TAKI···(137)

Some Synonymies in the Molluscan Family Cymatiidae by A. G. BEU·····Tadashige HABE···(146)

Pearl Culture in Lake Biwa by K. HAYASHI ·····Iwao TAKI···(160)

Die Perlen by F. HAAS (transl. by K. HAYASHI)·····Iwao TAKI···(160)

Some Noteworthy Marine Gastropoda from Southwestern Japan (III) by T. SHIKAMA ·····Tadashige HABE···(161)

Bibliographies on Observation and Preparation of Molluscan Radula ·····Kohman ARAKAWA···(162)

Miscellany

Memories of the late Dr. Taku KOMAI ·····Iwao TAKI···(164)

Dr. Taku KOMAI and we ·····Tokubei KURODA···(164)

Proceedings

Monthly meeting in Tokyo ·····(166)

VENUS
THE JAPANESE JOURNAL OF MALACOLOGY

VENUS: Vol. 31, No. 4 (1973)

目　　次

原　　著

日本産イトカケガイ科の新属新種（挿図 1～2）……常陸宮正仁・波部忠重…(135)
鳥島沖産エビスガイ属の新種（挿図 1～2）……笹生一雄・波部忠重…(137)
ハリアキアサトボラとそれと誤同されていたチリメンナルトボラ……波部忠重…(139)
福井県冠山産レンズガイ属の1新種（挿図 1～5）……東　正雄…(143)
瀬戸内海泥底における底生二枚貝の捕食者について（I）ヒメカノコアサリに
　対するハナツメタガイの捕食の影響（挿図 1～9；表 1）……向井　宏…(147)

資　　料

イソギンチャクヤドリガイの宿主（挿図 1）……波部忠重…(157)
センニンガイの産卵（挿図 1-2）……K. ラマムールティ・R. ナタラジャン…(158)

抄 録 と 紹 介

生物学御研究所編：相模湾貝類……(英文) 滝　巌…(137)
ニュー著：フジツガイ科の異名……波部忠重…(146)
林　一正著：琵琶湖の真珠養殖……滝　巌…(160)
ハース著　林　一正訳：真珠の話……滝　巌…(160)
鹿間時夫著：南西日本産の注目すべき海産巻貝類数種について（3）…波部忠重…(161)
［スズキ］著：腹足類2新種の記載……滝　巌・波部忠重…(161)
軟体動物の歯舌の観察並びに標本製作法に関する文献集……荒川好満…(162)

雑　　録

駒井卓先生の追悼……滝　巌…(164)
駒井卓先生と私達……黒田徳米…(164)

学 会 記 事

東京支部例会……(166)

日本貝類学会

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VENUS

THE JAPANESE JOURNAL OF MALACOLOGY

第32巻 第1号 Vol. 32, No. 1

目 次

原 著

新潟県産シブキツボ属の一新亜種（挿図1—6）……湊 宏…(1)

日本近海産チドリマスオガイ科——付：新種コベガイの記載（挿図1—4）……桜井欽一・波部忠重…(4)

紀伊半島切目埼沖産若干種の歯舌について——付：新種イモガイの記載（図版I；挿図1—11）……東 正雄…(9)

北海道宗谷岬産白亜紀オキナエビスガイ科の新種（図版II；挿図1—2）……蟹江康光・波部忠重…(19)

資 料

白山産オオミケマイマイの生殖腺知見（挿図1—2）……湊 宏…(25)

学 会 記 事

東京支部例会……(26)

Contents

Original Articles

A New Species of the Genus *Fukuia* (Pomatiopsidae) from Niigata Prefecture, Japan (Text-figs. 1-6)……Hiroshi MINATO…(1)

Family Mesodesmatidae of Japan and Adjacent Area with the Description of a New Species (Text-figs. 1-4)……Kin'ichi SAKURAI and Tadashige HABE…(4)

On the Radulae of Some Remarkable Gastropods from off Kirimesaki, Kii Peninsula, Japan, with the Description of a New Cone Shell (Plate I, Text-figs. 1-11)……Masao AZUMA…(9)

A New Species of the Cretaceous Pleurotomariid from Cape Soya, Northern Hokkaido, Japan (Plate II, Text-figs. 1-2)……Yasumitsu KANIE and Tadashige HABE…(19)

Short Note

Genital Notes on *Aegista* (*Plectotropis*) *omiensis* (PILSBRY, 1902) from Mt. Hakusan, Ishikawa Prefecture, Japan (Text-figs. 1-2)…Hiroshi MINATO…(25)

Proceedings

Monthly Meetings at Tokyo……(26)

昭和48年5月 May 1973

東京 Tokyo

VENUS
THE JAPANESE JOURNAL OF MALACOLOGY

第32巻 第2号 Vol. 32, No. 2

目 次

原 著

福岡県産ムシオイガイ属の新種（挿図1）……高橋五郎・波部忠重…27
ウミナボラ属の1新種，ミユキウミナボラ（図版III）……千葉 蘭児…29
紀伊及び土佐産3新種腹足類とトマヤガイ科の1稀種について（挿図 1—8）
……東 正雄…33
日本近海産の珍らしいイカ類について—II．アブライカ（新種）について（図版IV—V；
挿図 1—15）……奥谷喬司・上村清幸…39

資 料

エラブマイマイの現棲標本について（挿図 1—3）……湊 宏…49

抄 録

ロコフ著：北太平洋深海から採集された単殻類の1新種……奥谷 喬司…47

学 会 記 事

東京支部例会……51

CONTENTS

Original Articles

A New Alycaeid Species, *Chamalycaeus miyazakii* n. sp., from Kyushu, Japan (Text-fig. 1)……Goro TAKAHASHI and Tadashige HABE…(27)
Description of a New Species of the Genus *Volutopsius*, *V. pallidus* n. sp. (Buccinidae), from Northeastern Japan (Pl. III) ……Ranji TIBA…(29)
Three New Gastropods from off Kii Peninsula and Tosa Bay with a Record of a Rare Carditid Bivalve (Text-figs. 1-8)……Masao AZUMA…(33)
Rare and Interesting Squid from Japan-II. A New Species of the Genus *Nototodarus* from Japan (Oegopsida: Ommastrephidae) (Pls. IV-V; Text-figs. 1-15)……Takashi OKUTANI and Kiyoyuki UEMURA…(39)

Review & Abstract

A New Species of Monoplacophoran from the Abyssal North Pacific by F. J. ROKOP ……Takashi OKUTANI…(47)

Short Notes

Note on a Living Specimen of *Nesiohelix irrediviva* (Text-figs. 1-3)
……Hiroshi MINATO…(49)

Proceedings

Monthly Meetings at Tokyo……(51)

昭和48年7月 July 1973

東京 Tokyo

貝類学雑誌
VENUS
THE JAPANESE JOURNAL OF MALACOLOGY

第32巻 第3号 Vol. 32, No. 3

CONTENTS

Original Articles

A Small Collection of Land Snails from the Islet Group, Danjo-Gunto, off Kyushu, Japan (Text-Figs. 1-9) ……Tokubei KURODA…(55)

Descriptions of Two New Species of the Genus *Colus* (Plate VI) …… Ranji TIBA…(65)

Penetration by Polychaetes found in Fossil Shells of Bivalve Genera *Glycymeris* and *Anadara* (Plates Ⅶ-Ⅷ; Text-figs. 1-4; Table 1) …… Iwao KOBAYASHI and Masae OMORI…(70)

Histochemical Analysis of Mucus in Caudal Gland of *Laevicaulis alte* (FÉRUSSAC) and Seasonal Variation (Pulmonata: Vaginulidae) (Plate Ⅸ) …… Y. M. DALAL and G. T. PANDYA…(83)

Short Notes

Genital Studies of Japanese Land Snails— Ⅱ. The Genitalia of *Satsuma* (*Coniglobus*) *tadai* KURODA from Senkaku Islands (Tex-fig. 1) ……Hiroshi MINATO…(91)

Olivella japonica (Gastropoda: Olividae) Preys on Juvenile *Meretrix lamarcki* (Bivalvia: Veneridae)……Sakko HAMADA…(94)

Review and Abstract

Fossil land snails from Minamijima, Bonin Island by T. HABE …… Tadashige HABE…(64)

Taxonomic studies of the land snail family Succineidae by C. M. PATTERSON …… Hiroshi MINATO…(93)

Treatise on invertebrate paleontology, Mollusca 6, Bivalvia (3 of 3) by L. R. COX *et al.* ……Tadashige HABE…(96)

Indo-Pacific Pisaniinae and related buccinid genera by W. O. CERNOHORSKY and note on some Australian genera and species of the family Buccinidae by W. F. PONDER ……Tadashige HABE…(97)

A classification of the family Buccinidae from the North Pacific by T. HABE and J. SATO ……Tadashige HABE…(98)

Miscellany

Changes of names ……Tadashige HABE and Masao AZUMA…(68)

貝類学雑誌
VENUS
THE JAPANESE JOURNAL OF MALACOLOGY

Vol. 32, No. 3 (1973)

昭和48年12月 December 1973

目　　次

原　　著

男女群島産陸貝類（挿図1～9）……黒田徳米…(55)
ツムガイ類の2新種の記載（図版VI）……千葉圀児…(65)
タマキガイ属（*Glycymeris*）・リュウキュウサルボウ属（*Anadara*）の化石にみられる多毛類による穿孔（図版VII～VIII；挿図1～4；表1）
……小林貴雄・大森昌衛…(70)
[illegible]（図版IX；表1）……Y. M. ダラール・G. T. バンジャ…(83)

資　　料

日本産陸棲貝類の生殖器の研究—II．実開列島産タダマイマイの生殖器（挿図1）……湊　宏…(91)
チョウセンハマグリ稚貝の害敵ホタルガイの食性……浜田サツ子…(94)

抄　　録

波部忠重著：小笠原南島産陸産貝類の化石……波部忠重…(64)
パターソン著：ナカセノアラガイの分類学的研究……湊　宏…(93)
コックス他24共著：軟体動物二枚貝綱（その4）……波部忠重…(96)
セルノホルスキー著：インド太平洋産 Pisaninae 亜科と近縁のエゾバイ科の諸
[illegible]……波部忠重…(97)
波部忠重・佐藤純子共著：北太平洋産エゾバイ科の分類……波部忠重…(98)

雑　　録

学名及び和名の変更……波部忠重／東　正雄…(68)

Malacological Review, 1974, 7: 192-195

AUTHOR INDEX FOR MALACOLOGICAL PERIODICALS

page*

ABBOTT, R. Tucker, Delaware Museum of Natural History, Greenville, Delaware 19803, U.S.A. 175
ADDICOTT, Warren O., U.S. Geological Survey, Menlo Park, California 94025, U.S.A. 184
AGÓCSY, Pál, Termeszettudomany Múzeum Allattara, Baross ut. 13, Budapest VIII, Hungary 182
ARAKAWA, Kohman Y., Hiroshima Fisheries Experimental Station, Tomokura, Ondo, Aki-gun, Hiroshima, Japan 186
AZUMA, Masao, 1-42 Kamiyoshihara, Hishiomiya, Hyogo Prefecture, Japan 186, 188, 189, 190
BÁBA, Károly, Vár u. 6/I/5, Szeged, Hungary 181
BABRAKZAI, Noorullah, Department of Biological Sciences, University of Arizona, Tucson, Arizona 85721, U.S.A. 173
BABU, K.S., Department of Zoology, Sri Venkateswara University, Tirupati 517502 (A.P.), India 185
BERRY, E.G., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A. 183
BERTSCH, Hans, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118, U.S.A. 184
BONA, E. [no address given] 168
BOSS, Kenneth J., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A. 175, 185
BRANSON, Branley A., Department of Biological Sciences, Eastern Kentucky University, Richmond, Kentucky 40475, U.S.A. 183
BRODY, Michael S., The Bodega Marine Laboratory, University of California, Bodega Bay, California 94923, U.S.A. 185
BURCH, J.B., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A. 173, 174
CABLE, Wayne D., National Marine Fisheries Service, Middle Atlantic Coastal Fisheries Center, Milford Laboratory, Milford, Connecticut 06460, U.S.A. 175
CALOW, P., Zoology Department, University of Glasgow, Glasgow, Scotland, U.K. 177
CAMP, Mark J., Department of Geology and Mineralogy, Ohio State University, Columbus, Ohio 43210, U.S.A. 183
CAPROTTI, Erminio, Via L.B. Alberti 12, 20149 Milano, Italy 170
CARLTON, James T., Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118, U.S.A. 185
CATE, Crawford N., Invertebrate Zoology, Los Angeles County Museum of Natural History, Los Angeles, California 90007, U.S.A. 184
CESARI, P. [no address given] 170
CHICHESTER, Lyle F., Department of Biological Sciences, Central Connecticut State College, New Britain, Connecticut 06050, U.S.A. 183
COURI, Claydon C., Geology Department, Kent State University, Kent, Ohio 44240, U.S.A. 183
COWAN, I. McTaggart [no address given] 184
CROWELL, H.H., Department of Entomology, Oregon State University, Corvallis, Oregon 97331, U.S.A. 177
DALAL, Y.M., Department of Biology, Gujarat College, Ahmedabad-6, India 190
DEMIAN, Emile S., Department of Zoology, Faculty of Science, Ain Shams University, Cairo, Egypt 174
DINAMANI, P., Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington, New Zealand 172
DIX, Trevor G., Fisheries Research Laboratory, Crayfish Point, Taroona, Tasmania 7006, Australia 172
EMERSON, William K., Department of Living Invertebrates, The American Museum of Natural History, Central Park West at 79th, New York, New York 10024, U.S.A. 184
FALKNER, Gerhard, Konrad Peutingerstr. 4, D-8 München 25, German Federal Republic 168
FARLEY, J., Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada 177
FELDMAN, Shelley L., Biology Department, Northeastern University, Boston, Massachusetts 02115, U.S.A. 173
FERREIRA, Antonio J., Beta Research Oceanographic Laboratories, Inc., 2060 Clarmar Way, San Jose, California 95128, U.S.A. 184
FOSTER, G.R., Box 659, 100 Mile House, British Columbia, Canada 169
FRALICK, Richard A., Jackson Estuarine Laboratory, University of New Hampshire,

*Page numbers, this issue of *Malacological Review*.

page

Adams Point, Durham, New Hampshire 03824, U.S.A. 175
FRANCHINI, Dario A., 37, Via Cremona, 46100 Mantova, Italy 170
FULLINGTON, Richard W., Dallas Museum of Natural History, P.O. Box 26193, Fair Park Station, Texas 75226, U.S.A. 175
GELPERIN, Alan, Department of Biology, Princeton University, Princeton, New Jersey 08540, U.S.A. 173
GETZ, Lowell, Department of Zoology, University of Illinois, Urbana, Illinois 61801, U.S.A. 176, 183
GHISOTTI, Fernando, Via Giotto 9, I-20145, Milano, Italy 170
GILMOUR, T.H.J., Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada 173
GIROD, Alberto, Via Savona 94/A, 20144-Milano, Italy 168
GOODMAN, Dan, Department of Environment, Fisheries Service, 1090 West Pender Street, Vancouver, British Columbia, Canada 185
GÖTTING, K.-J., Zoologisches Institut der Justus Liebig-Universität, Stephanstr. 24, D-63 Giessen, German Federal Republic 168
GOUDSMIT, Esther M., Biology Department, Oakland University, Rochester, Michigan 48063, U.S.A. 173
HABE, Tadashige, National Science Museum, Ueno Park, Tokyo 160, Japan 186, 188, 189, 190
HADŽIŠČE, Slave, Hydrobiological Institute, 97300 Ohrid, Macedonia, Yugoslavia 173
HAMADA, Sakko [no address given] 190
HANIFFA, M.A., Madurai University P.G. Centre, Sri Palaniandavar Arts College, Palni, South India 185
HARMAN, Willard N., New York State University College at Oneonta, Oneonta, New York 13820, U.S.A. 175
HARVEY, Paul H., Department of Zoology, University College, Swansea, Wales, U.K. 177
HEARD, William H., Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306, U.S.A. 173
HEMBROW, Deborah, Department of Zoology, University of Reading, Reading, U.K. 177
HOUBRICK, Richard, Supervisor for Invertebrates, Smithsonian Oceanographic Sorting Center, Smithsonian Institution, Washington, D.C. 20560, U.S.A. 176
HUBRICHT, Leslie, 4026 35th Street, Meridian, Mississippi 39301, U.S.A. 173
JACOBSON, Morris K., American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A. 175, 176, 183, 185
KAMEL, E.G., Department of Zoology, Faculty of Science, Ain Shams University, Cairo, Egypt 174
KANIE, Yasumitsu, Yokosuka City Museum, Yokosuka, Japan 188
KANJILAL, S., Geology Department, Banaras Hindu University, Varanasi-5 (U.P.), India 177
KARROW, P.F., Department of Earth Sciences, University of Waterloo, Waterloo, Ontario, Canada 184
KEEN, A. Myra, Department of Geology, Stanford University, Stanford, California 94305, U.S.A. 185
KHOO, Hong-Woo, Department of Zoology, University of Singapore, Singapore 185
KOBAYASHI, Iwao, Department of Geology and Mineralogy, Faculty of Science, Niigata University, Niigata, Japan 190
KRAKAUER, Janet M., Department of Biology, Hollins College, Virginia 24020, U.S.A. 185
KROLOPP, E., Ungarische Geologische Anstalt, Népstadion u. 14, Budapest XIV, Hungary 181, 182
KUES, Barry S., Department of Geology, Indiana University, Bloomington, Indiana 47401, U.S.A. 184
KUIJPER, W.J., De Lannoystr. 101, Den Haag, The Netherlands 169
KUMAR, T. Pavan, Department of Zoology, Sri Venkateswara University, Tirupati 517502 (A.P.), India 185
KURIS, Armand M., The Bodega Marine Laboratory, University of California, Bodega Bay, California 94923, U.S.A. 185
KURODA, Tokubei, 41, Tanaka, Minami-Okubo-cho, Sakyo, Kyoto, Japan 186, 190
La ROCQUE, Aurèle, Department of Geology, Ohio State University, Columbus, Ohio 43210, U.S.A. 183
LAWS, Helene M., South Australian Museum, Adelaide, Australia 172
LEWIS, Hal, Department of Malacology, Academy of Natural Sciences, Philadelphia, Pennsylvania 19103, U.S.A. 176
LIANG, Yung-San, Museum of Zoology, The University of Michigan, Ann Arbor,

page

Michigan 48104, U.S.A. 183
LINDSAY, G.K., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A. 174
LOOSJES, F.E., Fossenlaan 4, Wageningen, The Netherlands 168
LOOSJES - van Bemmel, A.C.W., Wageningen, The Netherlands 168
LoVERDE, Philip T., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A. 174
MALDONADO QUILES, A. [no address given] 170
MARIANI, M., Via N. Battaglia 23, 20121, Milano, Italy 168
MASAHITO, Prince [ref. T. Habe, National Science Museum, Ueno Park, Tokyo, Japan] 186
MELVILLE, R.V., Secretary, ICZN, c/o British Museum (Natural History), London SW7 5BD, U.K. 185
MERDSOY, B., Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada 177
MIENIS, H.K., The Hebrew University of Jerusalem, Department of Zoology, Section Mollusca, Jerusalem, Israel 169
MILLER, Walter B., Department of Biological Sciences, University of Arizona, Tucson, Arizona 85721, U.S.A. 173
MINATO, Hiroshi, Kumano Senior High School, Kamitonda-cho, Wakayama Prefecture, Japan 188, 189, 190
MOAYEDPOUR, E. [no address given] 168
MUKAI, Hiroshi, Ocean Research Institute, University of Tokyo, Tokyo, Japan 186
MURTHY, Ch. Radha Krishna, Department of Zoology, Sri Venkateswara University, Tirupati 517502 (A.P.), India 185
NATARAJAN, R., Centre of Advanced Study in Marine Biology, Porto Novo, Tamilnadu, India 186
NISBET, R.H., Department of Physiology, Electron Microscope Unit, Royal Veterinary College, London NW1 0TU, U.K. 177
NORDSIECK, Hartmut, Johannesstr. 38, D-722 Schwenningen, German Federal Republic 168
NYBAKKEN, James, Moss Landing Marine Laboratories, Moss Landing, California 95039, U.S.A. 184
OKUTANI, Takashi, Tokai Regional Fisheries Research Laboratory, Tokyo, Japan 189
OLD, William E., Jr., Department of Living Invertebrates, The American Museum of Natural History, New York, New York 10024, U.S.A. 176
OMORI, Masae, Faculty of Sciences, Tokyo University of Education, Tokyo, Japan 190
PALACIO, Francisco J., University of Miami, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida 33149, U.S.A. 175
PANDIAN, T.J., Madurai University P.G. Centre, Sri Palaniandavar Arts College, Palni, South India 185
PANDYA, G.T., Department of Biology, Gujarat College, Ahmedabad-6, India 190
PARKER, Marilyn, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A. 174
PATTERSON, C.M., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A. 173
PETTITT, C., Manchester Museum, The University, Manchester M/C M13 9PL, U.K. 177
PINTÉR, István [no address given] 180
PINTÉR, László, Pasareti ut. 137, Budapest II, Hungary 181
PODANI, János [no address given] 182
PONDER, W.F., The Australian Museum, 6-8 College Street, Sydney, Australia 172
PRIOR, David J., School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506, U.S.A. 173
RAMAMOORTHI, K., Centre of Advanced Study in Marine Biology, Porto Novo, Tamilnadu, India 186
REGTEREN ALTENA, C.O., van, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands 169
REISCHÜTZ, Peter L. [no address given] 168
REX, Michael A., Department of Biology, University of Massachusetts - Boston, Boston, Massachusetts 02116, U.S.A. 175
RINALDI, Emidio [no address given] 170
ROSE, Kenneth D., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A. 176
ROSS, June R.P., Department of Biology, Western Washington State College, Bellingham, Washington 98225, U.S.A. 185

	page
RUDOLPH, Paul H., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.	173
SAKURAI, Kin'ichi [no address given]	188
SASAO, Kazuo [no address given]	186
SCHLICKUM, W. Richard, Hansaring 32, D-5 Köln, German Federal Federal Republic	168
SCHÜTT, Hartwig, D-4 Düsseldorf-Benrath, Haydnstrasse 50, Germany	169
SEAPY, Roger R., Department of Population and Environmental Biology, University of California, Irvine, California 92664, U.S.A.	184
SENSEMAN, D., Department of Biology, Princeton University, Princeton, New Jersey 08540, U.S.A.	173
SEVO, Slavica, Station de Zoologie appliquée de l'Etat, Gembloux, Belgium	173
SHRADER, Amy L., 501 South Market Street, Waverly, Ohio 45690, U.S.A.	173
SINGH, C.S.P., Geology Department, Banaras Hindu University, Varanasi-5 (U.P.), India	177
SMITH, Brian J., Curator of Invertebrates, National Museum of Victoria, Melbourne, Victoria, Australia	172
SODEMAN, William A., Jr.; University of Arkansas, School of Medicine, Department of Internal Medicine, 4301 West Markham, Little Rock, Arkansas 72201, U.S.A.	175
SOLEM, Alan, Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, U.S.A.	172, 184
SPOEL, S., van der, Institute for Taxonomical Zoology, Amsterdam, The Netherlands	169
STERN, Edward M., Department of Zoology and Physiology, Louisiana State University, Baton Rouge, Louisiana 70803, U.S.A.	176
STIVA, A. [no address given]	169
STRAUCH, Friedrich, Geologisches Institut der Universität, Zülpicherstr. 49, D-5 Köln, German Federal Republic	168
SWAMI, K.S., Department of Zoology, Sri Venkateswara University, Tirupati 517502 (A.P.), India	185
SZIGETHY, Anna [no address given]	181
TAKAHASHI, Goro [no address given]	189
TAKI, Iwao, 48 Nakayamacho, Kamikamo, Kitaku, Kyoto, Japan	186
TALMADGE, Robert R., Field Associate, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118, U.S.A.	185
TANG, Isabel, Department of Zoology, University of Singapore, Singapore	185
TE, George A., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.	173
TEMNIKOW, Nicolas K., Bodega Marine Laboratory, University of California, Bodega Bay, California 94923, U.S.A.	185
TIBA, Ranji [no address given]	189, 190
TOMPA, Alex S., Department of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.	173
TURGEON, Kenneth W., Jackson Estuarine Laboratory, University of New Hampshire, Adams Point, Durham, New Hampshire 03824, U.S.A.	175
UEMURA, Kiyoyuki, Chiba Prefectural Fisheries Experimental Station, Tateyama, Japan	189
UKOLI, F.M.A., Department of Zoology, University of Ibadan, Ibadan, Nigeria	173
VAIL, Virginia A., Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306, U.S.A.	173
Van der SCHALIE, Henry, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.	183
VARGA, András, Mátra Múzeum, Kossuth u. 40, Gyöngös, Hungary	182
VÁSÁRHELYI, István [no address given]	181
VASS, Anna [no address given]	181
VOSS, Gilbert L., Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Flroida 33149, U.S.A.	184
WALTER, Jakob, Zoologisches Museum der Universität Zurich, Switzerland	168
WEBB, Glenn R., Kutztown State College, Kutztown, Pennsylvania 19530, U.S.A.	171
WHITLEY, Gilbert P., The Australian Museum, 6-8 College Street, Sydney, Australia	172
WILSON, Barry R., Western Australian Museum, Perth, Australia	172
WOLFSON, Fay Henry, Research Associate, San Diego Natural History Museum, San Diego, California 92112, U.S.A.	185
WU, S.-K., University of Colorado Museum, Boulder, Colorado 80302, U.S.A.	174
ZILCH, A., Senckenberg Museum, Senckenberg-Anlage 25, D-6 Frankfurt/M. 1, Germany	168
ZISCHKE, J.A., Biology Department, St. Olaf College, Northfield, Minnesota 55057, U.S.A.	185

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* * * * * * *

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INDEX TO SCIENTIFIC NAMES

Abida, 1-14
frumentum, 1-14
secale, 1, 3, 5, 10, 11, 14
abyssinicus, Bulinus, 56
abyssinicus, Physopsis, 56
Acanthinula, 8
aculeata, 8
Acanthochitona, 163, 164
balesae, 163
bonairensis, 163
elongata, 163
interfissa, 163
rhodea, 164
Achatina, 51
fulica, 51
acicula, Cecilioides, 9, 10, 11, 13
Acme, 1-14
inchoata, 1-14
lineata, 1-4, 14
Acmidae, 1
Acteonidae, 134
aculeata, Acanthinula, 8
acuta, Physa, 43, 44
alexandrina, Biomphalaria, 15-24
Alexia, 1-14
denticulata, 1-14
myosotis, 1, 5, 6, 13, 14
alternata, Anguispira, 33, 35, 36, 50
alternata crassa, Anguispira, 33
alternata macneilli, Anguispira, 33
alternata strongylodes, Anguispira, 33
Amblema, 41
Amblemidae, 41
Amerianna, 43
amphitrite, Balanus, 107
ancillaria, Physa, 43
Ancylus, 127-132
fluviatilis, 127-132
fluviatilis strigatus, 127, 131
Anguispira, 33, 35, 36, 50
alternata, 33, 35, 36, 50
alternata crassa, 33
alternata macneilli, 33
alternata strongylodes, 33
clarki, 33
strongylodes, 33
angulifera, Littorina scabra, 105-125
Anisomyaria, 49
Anisus, 13
rotundatus, 13
Anodonta, 41
Anodontites, 41
Anomiidae, 49
Ancylastrum, 131
Ancylidae, 127
Aplexa, 43, 44
hypnorum tryoni, 44
marmorata, 44
Aplysia, 52
californica, 52
appressa, Lymnaea stagnalis, 26-31
approxima, Retinella, 34
Arca, 49
noea, 49
Arcidae, 49
Arcoida, 49
arietina, Chelidonopsis, 41
Ariolimax, 51
californica, 51
Arion, 51
ater, 51
hortensis, 51
Ashmunella, 37, 38
chiricahuana, 37, 38
proxima, 37
Aspatharia, 41
aspersa, Helix, 51
Asperula, 2
odorata, 2
Assiminea, 13
grayana, 13
atakana, Littorina, 106
ater, Arion, 51
Atyidae, 134
Aulacopoda, 50
aurea, Physa, 44
auricularia, Radix, 26-31, 47
Austropeplea, 25-27, 47
ollula, 26, 27
Balanus, 107
amphitrite, 107
balesae, Acanthochitona, 163
barbatus, Modiolus, 49
Basommatophora, 25
batchi, Philomycus, 33
Bathiomphalis, 13
contortus, 13
bermudensis, Ischnochiton, 163
Biomphalaria, 15-24
alexandrina, 15-24
obstructa, 23
peregrina, 23
pfeifferi, 15-24
straminea, 23
sudanica, 15-24
tenagophila, 23
bisdosus, Philomycus, 33
Bithynia, 13
leachi, 13
tentaculata, 13
Bivalvia, 49
bonairensis, Acanthochitona, 163
boogii, Ischnochiton, 163, 164
bronniana, Lima, 49
bryanti nigrimontanus, Discus, 33
Buccinum, 13
undatum, 13
budapestensis, Milax, 51
Bulimnea, 25-27, 30, 47
megasoma, 26, 27, 30
Bulinus, 15, 43, 45, 46, 54, 55, 56
abyssinicus, 56
globosus, 45
hexaploidus, 45, 56

natalensis, 45, 46
octoploidus, 45, 56
scalaris, 45
sericinus, 56
tropicus, 45, 46, 56
truncatus sericinus, 45, 46
truncatus truncatus, 45, 46, 55, 56
Burnupia, 127, 130, 131
capensis, 127, 130, 131
burringtoni, Glyphyalinia, 33
burringtoni, Mesodon, 34
burringtoni, Stenotrema, 34
Caelatura, 41
Cafferia, 41
californica, Aplysia, 52
californica, Ariolimax, 51
californica, Pleurobranchaea, 52
Callistochiton, 164
shuttleworthianus, 164
Campeloma, 42
geniculum, 42
rufum, 42
tannum, 42
Camptoceras, 43
cancellinus, Distortrix, 133-135
capensis, Burnupia, 127, 130, 131
capsella, Paravitrea, 34
carinatus, Tropidiscus, 13
carolinianus, Philomycus, 33
Carychium, 8, 9, 33
floridanum, 33
mexicanum, 33
minimum, 9
tridentatum, 8, 9
Castalia, 41
Catinella, 52
vermeta, 52
Cecilioides, 9, 10, 11, 13
acicula, 9, 10, 11, 13
cellarius, Oxychilus, 13
Cepaea, 8, 10, 50
hortensis, 8, 10
nemoralis, 10, 50
Cephalaspidea, 134
cespitum, Helicella, 13
Chaetopleura, 164
Chelidonopsis, 41
arietina, 41
chiricahuana, Ashmunella, 37, 38
Chthamalus, 107
circumstriata, Glyphyalinia, 33
circumstriata, Retinella, 33
clarki, Anguispira, 33
clathrata, Distorsio, 133
Clausilia, 2, 8, 9, 10, 11
dubia, 2
dubia obsoleta, 2
nigricans, 8, 9
parvula, 8, 9, 10, 11
clingmani, Glyphyalinia, 34
clingmani, Retinella, 34
Cochlicella, 13
acuta, 13
Cochlicopa, 8-11, 13
lubrica, 8-11, 13
Cochlodina, 9, 11
laminata, 9, 11
columella, Pseudosuccinea, 26, 27, 29, 30, 33
concentricus, Uncancylus, 127, 130, 131
concordialis, Succinea, 33
contectoides, Viviparus, 42
contortus, Bathiomphalis, 13
corvus, Stagnicola, 31
costata, Nassa, 133
costata, Vallonia, 9-11, 13
crassa, Anguispira alternata, 33
Crassostrea, 107
virginica, 107
cristata, Valvata, 13
crystallina, Vitrea, 8-11
cubensis, Physa, 43, 44
Cumberlandia, 41
cumberlandiana, Glyphyalinia, 33
cylindracea, Lauria, 10, 11, 13
Cymatidae, 133
Cymatilesta, 133
spengleri, 133
Cymatium, 133
nicobaricum, 133
pileare, 133
denticulata, Alexia, 1-14
Deroceras, 51
reticulatum, 51
derochetus, Mesomphix, 34
diaphanus, Laevapex, 127, 130, 131
Diastropha, 43
Digenea, 165
diomedia, Tritonia, 52
Diplodon, 41
Discus, 8, 9, 13, 33
bryanti nigrimontanus, 33
nigrimontanus, 33
patulus, 33
patulus edentulus, 33
rotundatus, 8, 9, 13
Distorsio, 133
clathrata, 133
Distortrix, 133-135
cancellinus, 133-135
doliolum, Orcula, 9, 11
dorsata, Nassa, 133, 134
downieanus, Mesodon, 34
draparnaudi, Oxychilus, 8, 10, 11, 13
dubia, Clausilia, 2
dubia obsoleta, Clausilia, 2
edentulus, Discus patulus, 33
edulis, Ostrea, 49
elegans, Pomatias, 8, 9, 11
Elliptio, 41
Ellobiidae, 1
elodes, Stagnicola, 27, 29, 31
elongata, Acanthochitona, 163
emarginata, Stagnicola, 27, 30, 31
Ena, 8
obscura, 8
Endodontidae, 35
Ensidens, 41
erythronotus, Ischnochiton, 163
Etheria, 41, 42
elliptica, 41
Etheriidae, 41
Euconulus, 9
fulvus, 9
Fagetum, 2
felina, Omalonyx, 48, 52
Ferrissia, 127, 129, 131

rivularis, 127, 129
filosa, Rhodacmea, 127-132
flava, Littorina, 119
flavus, Limax, 51
floridanum, Carychium, 33
fluviatilis, Ancylus, 127-132
fluviatilis strigatus, Ancylus, 127, 131
fontinalis, Physa, 43, 44
forsheyi, Succinea, 33
Fossaria, 25-31, 48
obrussa, 26-31
truncatula, 28, 31
fosteri, Pallifera, 33
frumentum, Abida, 1-14
Fruticicola, 10, 11
fruticum, 10, 11
fruticum, Fruticicola, 10, 11
fulica, Achatina, 51
fulvus, Euconulus, 9
gaederopus, Spondylus, 49
Galba, 28
Gastropoda, 105
geniculum, Campeloma, 42
georgianus, Viviparus, 42
glassi, Stenotrema, 34
globosa, Physa, 43
globosus, Bulinus, 45
globosus, Mexomphix, 34
globosus, Physopsis, 45, 46
Glyphyalinia, 33, 34
burringtoni, 33
circumstriata, 33
clingmani, 34
cumberlandiana, 33
raderi, 33
rhoadsi, 33
roanensis, 33
wheatleyi, 33
Gonidea, 41
goodrichi, Physa, 44
gracile, Opeas, 136
grayana, Assiminea, 13
gyrina hildrethiana, Physa, 44
gyrina, Physa, 43
haematobium, Schistosoma, 15, 45, 56
Haliotis, 50
Helicella, 8, 10, 11, 13
cespitum, 13
itala, 8, 10, 11
profuga, 13
virgata, 13
Helicodonta, 8-11
obvoluta, 8-11
Helix, 9, 11, 50, 51, 53
aspersa, 51
pomatia, 9, 11, 50, 51, 53
hemphilli marmorea, Pallifera, 33
hendersoni, Physa, 44
hendersoni, Physa pomilia, 43
hexaploidus, Bulinus, 45, 56
hexaploidus, Isidora, 45
hians, Lima, 49
hildrethiana, Physa gyrina, 44
hirsutum, Stenotrema, 34
hirundo, Pteria, 49
hispida, Trichia, 8, 11, 13
Holopoda, 50
hortensis, Arion, 51
hortensis, Cepaea, 8, 10
hupensis, Oncomelania, 57
Hydatina, 133-135
velum, 133-135
Hydatinidae, 134
Hydrobia, 13
jenkinsi, 13
stagnorum, 13
ulvae, 13
hypnorum tryoni, Aplexa, 44
Hyria, 41
Hyridella, 41
Hyriopsis, 41
Hyriidae, 41
incarnata, Zenobiella, 8, 10
inchoata, Acme, 1-14
inflata, Physa, 43, 44
Inflectarius, 34
subpalliatus, 34
integra, Physa, 43, 44
interfissa, Acanthochitona, 163
Iphigena, 11
ventricosa, 11
irrorata, Littorina, 105-125
Ischnochiton, 163, 164
bermudensis, 163
boogii, 163, 164
erythronotus, 163
limaciformis, 163
liozonis, 164
pseudovirgatus, 163
purpurascens, 163
Isidora, 43, 45, 46, 54
hexaploidus, 45
natalensis, 45, 46
octoploidus, 45
tropicus, 45, 46
truncatus sericinus, 45, 46
truncatus truncatus, 45, 46
Isidorella, 43
itala, Helicella, 8, 10, 11
japonicum, Schistosoma, 57
jenkinsi, Hydrobia, 13
Katherina, 37
tunicata, 37
labrosum, Stenotrema, 34
Laevapex, 127, 130, 131
diaphanus, 127, 130, 131
lamarrei, Macrobrachium, 136
laminata, Cochlodina, 9, 11
lammellatum, Punctum, 33
Lanx, 28
laphami, Physa, 44
Lauria, 10, 11, 13
cylindracea, 10, 11, 13
leachi, Bithynia, 13
Leila, 41
Lepidochitona, 163, 164
liozonis, 163
montoucheti, 164
rosea, 163, 164
tropica, 164
Lima, 49
bronniana, 49
hians, 49
scabra, 49
subauriculata, 49
limaciformis, Ischnochiton, 163, 164

Limax, 50, 51
flavus, 51
maximus, 50
Limidae, 49
lineata, Acme, 1-4, 14
Lioplax, 42, 43
pilsbryi, 42
subcarinata occidentalis, 43
liozonis, Ischnochiton, 164
liozonis, Lepidochitona, 163
lithodora, Paravitrea placentula, 34
littorea, Littorina, 106
Littorina, 105-125
atakana, 106
flava, 119
irrorata, 105-125
littorea, 106
obtusata, 106
picta, 106, 123
pintado, 106, 123
planaxis, 106
saxatilis, 106
scabra angulifera, 105-125
scabra scabra, 106, 120, 123
sitkana, 106
lubrica, Cochlicopa, 8-11, 13
luteola, Radix, 31
Lymnaea, 9, 10, 13, 25-31, 47, 48
peregra, 10, 13
stagnalis, 28, 31, 47
stagnalis appressa, 26-31
truncatula, 9
Lymnaeidae, 25, 28
macneilli, Anguispira alternata, 33
Macrobrachium, 136
lamarrei, 136
macroschisma, Pododesmus, 49
major, Vitrina, 9, 10, 13
mangle, Rhizophora, 105, 107
mansoni, Schistosoma, 23, 24, 57
Margaritifera, 41
Margaritiferidae, 41
marmorata, Aplexa, 44
marmorata, Stenophysa, 43
marmorea, Pallifera, 33
marmorea, Pallifera hemphilli, 33
maximus, Limax, 50
maximus, Pecten, 49
Megalonaias, 41, 42
megaphalica, Pallifera, 33
megasoma, Bulimnea, 26, 27, 30
Mercurialis, 2
perennis, 2
Mesodon, 34
burringtoni, 34
downieanus, 34
mitchellianus, 34
subpalliatus, 34
verus, 34
Mesomphix, 34
derochetus, 34
globosus, 34
ruidus, 34
vulgatus, 34
Mesurethra, 50
mexicanum, Carychium, 33
michiganensis, Physa, 44
Milax, 51
budapestensis, 51
minimum, Carychium, 9
Miratesta, 43
mitchellianus, Mesodon, 34
Modiolus, 49
barbatus, 49
montoucheti, Lepidochitona, 164
multilineata, Triodopsis, 50
muscorum, Pupilla, 10, 11, 13
Mutela, 41
Mutelacea, 41, 42
Mutelidae, 41
Mycetopoda, 41
Mycetopodidae, 41
myosotis, Alexia, 1, 5, 6, 13, 14
Mystus, 136
Mytilidae, 49
Mytiloida, 49
Nassa, 133-134
costata, 133
dorsata, 133-134
thersites, 133
Nassidae, 133
natalensis, Bulinus, 45, 46
natalensis, Isidora, 45, 46
nemoralis, Cepaea, 10, 50
nicklinii, Physa, 43, 44
nicobaricum, Cymatium, 133
nigricans, Clausilia, 8, 9
nigrimontanus, Discus, 33
nigrimontanus, Discus bryanti, 33
nitida, Segmentina, 13
nitidula, Retinella, 8, 9
nitidus, Zonitoides, 13
nobilis, Pinna, 49
noea, Arca, 49
oblonga, Succinea, 9
obrussa, Fossaria, 26-31
obscura, Ena, 8
obsoleta, Clausilia dubia, 2
obstructa, Biomphalaria, 23
obtusata, Littorina, 106
obvoluta, Helicodonta, 8-11
occidentalis, Lioplax subcarinata, 43
octoploidus, Bulinus, 45, 56
octoploidus, Isidora, 45
odorata, Asperula, 2
ohirai, Paragonimus, 57
ollula, Austropeplea, 26-29
Omalonyx, 48, 52
felina, 48, 52
unguis, 48
Oncomelania, 57
hupensis, 57
Opeas, 136
gracile, 136
Opisthobranchia, 134
Orcula, 9, 11
doliolum, 9, 11
Orthurethra, 50
Ostrea, 49
edulis, 49
Ostreidae, 49
Oxychilus, 8, 10, 11, 13
cellarius, 13
draparnaudi, 8, 10, 11, 13
Oxyloma, 52
retusa, 52

Pallifera, 33
hemphilli marmorea, 33
fosteri, 33
marmorea, 33
megaphalica, 33
tornescalis, 33
palustris, Stagnicola, 28
Paragonimus, 57
ohirai, 57
Paravitrea, 34
capsella, 34
placentula, 34
placentula lithodora, 34
parkeri, Physa, 43, 44
parvula, Clausilia, 8, 9, 10, 11
parvulus, Trachydermon, 164
Patera, 34
subpalliatus, 34
patulus, Discus, 33
patulus edentulus, Discus, 33
Pecten, 49
maximus, 49
Pectinidae, 49
peregra, Lymnaea, 10, 13
peregra, Radix, 31
peregrina, Biomphalaria, 23
perennis, Mercurialis, 2
pfeifferi, Biomphalaria, 15-24
Philinidae, 134
Philomycus, 33
batchi, 33
bisdosus, 33
carolinianus, 33
venustus, 33
Physa, 43, 44
acuta, 43, 44
ancillaria, 43
aurea, 44
cubensis, 43, 44
fontinalis, 43, 44
globosa, 43
goodrichi, 44
gyrina, 43
gyrina hildrethiana, 44
hendersoni, 44
inflata, 43, 44
integra, 43, 44
laphami, 44
michiganensis, 44
nicklinii, 43, 44
parkeri, 43, 44
pomilia, 43, 44
pomilia hendersoni, 43
sayii, 43, 44
skinneri, 43, 44
virgata, 44
Physastra, 43
Physopsis, 43, 45, 46, 56
abyssinicus, 56
globosus, 45, 46
Physunio, 41
picta, Littorina, 106, 123
pileare, Cymatium, 133
pilsbryi, Lioplax, 42
Pilsbryoconcha, 41
pintado, Littorina, 106, 123
Pinna, 49
nobilis, 49
Pinnidae, 49
piscinalis, Valvata, 13
placentula lithodora, Paravitrea, 34
placentula, Paravitrea, 34
planaxis, Littorina, 106
Planorbidae, 131
planorbis, Tropidiscus, 13
Platyhelminthes, 165
Plectomerus, 41
Plesiophysa, 43
Pleurobema, 41
Pleurobranchaea, 52
californica, 52
Pneumonopoma, 2
Pododesmus, 49
macroschisma, 49
Polygyra, 34
rexroadensis, 34
texasiana, 34
Polyplacophora, 163, 164
pomatia, Helix, 9, 11, 50, 51, 53
Pomatias, 8, 9, 11
elegans, 8, 9, 11
pomilia hendersoni, Physa, 43
pomilia, Physa, 43, 44
Prisodon, 41
profuga, Helicella, 13
Prosobranchia, 105, 133
proxima, Ashmunella, 37
Pseudisidora, 43
Pseudodon, 41
Pseudospatha, 41
tanganyikensis, 41
Pseudosuccinea, 25-27, 29, 30, 33, 48
columella, 26, 27, 29, 30, 33
pseudovirgatus, Ischnochiton, 163
Pteria, 49
hirundo, 49
Pteriidae, 49
Pterioida, 49
Pteriomorpha, 49
pulchella, Vallonia, 8, 9, 13
Pulmonata, 127
Punctum, 8, 9, 13, 33
lammellatum, 33
pygmaeum, 8, 9, 13
smithi, 33
Pupilla, 10, 11, 13
muscorum, 10, 11, 13
purpurascens, Ischnochiton, 163
pusilla, Vertigo, 10
putris, Succinea, 8, 10, 52
pygmaea, Vertigo, 8, 10, 11
pygmaeum, Punctum, 8, 9, 13
Pyramidula, 10
rupestris, 10
Pyrgophysa, 45, 46
scalaris, 45, 46
raderi, Glyphyalinia, 33
Radix, 25-32, 47
auricularia, 26-31, 47
luteola, 31
peregra, 31
relicta, 25-32, 47
Radsiella, 164
relicta, Radix, 25-32, 47
reticulatum, Deroceras, 51
Retinella, 8, 9, 33, 34

approxima, 34
circumstriata, 33
clingmani, 34
nitidula, 8, 9
wheatleyi, 33
retusa, Oxyloma, 52
rexroadensis, Polygyra, 34
Rhizophora, 105, 107
mangle, 105, 107
rhodacme, Rhodacmea, 127-132
Rhodacmea, 127-132
filosa, 127-132
rhodacme, 127-132
rhodea, Acanthochitona, 164
rhoadsi, Glyphyalinia, 33
rivularis, Ferrissia, 127, 129
roanensis, Glyphyalinia, 33
rosea, Lepidochitona, 163, 164
rotundatus, Anisus, 13
rotundatus, Discus, 8, 9, 13
rufum, Campeloma, 42
rugosula, Vertigo, 33
ruidus, Mesomphix, 34
rupestris, Pyramidula, 10
saxatilis, Littorina, 106
sayii, Physa, 43, 44
Scabies, 41
scabra angulifera, Littorina, 105-125
scabra, Lima, 49
scabra, Littorina scabra, 106, 120, 123
scabra scabra, Littorina, 106, 120, 123
scalaris, Bulinus, 45
scalaris, Pyrgophysa, 45, 46
Schistosoma, 15, 23, 24, 45, 56, 57
haematobium, 15, 45, 56
japonicum, 57
mansoni, 23, 24, 57
secale, Abida, 1, 3, 5, 10, 11, 14
Segmentina, 13
nitida, 13
sericea, Trichia, 8, 9, 13
sericinus, Bulinus, 56
sericinus, Bulinus truncatus, 45, 46
sericinus, Isidora truncatus, 45, 46
shuttleworthianus, Callistochiton, 164
Sigmurethra, 50
sitkana, Littorina, 106
skinneri, Physa, 43, 44
smithi, Punctum, 33
Spartina, 105, 107, 112, 113, 118, 124
spengleri, Cymatilesta, 133
Spiralina, 13
vortex, 13
Spondylidae, 49
Spondylus, 49
gaederopus, 49
stagnalis appressa, Lymnaea, 26-31
stagnalis, Lymnaea, 28, 31, 47
Stagnicola, 25, 27-29, 31, 48
corvus, 31
elodes, 27, 29, 31
emarginata, 27, 30, 31
palustris, 28
stagnorum, Hydrobia, 13
Stenophysa, 43
marmorata, 43
Stenoplax, 164
Stenotrema, 34
burringtoni, 34
glassi, 34
hirsutum, 34
labrosum, 34
straminea, Biomphalaria, 23
strigatus, Ancylus fluviatilis, 127, 131
strongylodes, Anguispira, 33
strongylodes, Anguispira alternata, 33
Strophitus, 42
Stylommatophora, 35, 59, 136
subauriculata, Lima, 49
subcarinata occidentalis, Lioplax, 43
subpalliatus, Inflectarius, 34
subpalliatus, Mesodon, 34
subpalliatus, Patera, 34
Subulinidae, 136
Succinea, 8, 9, 10, 33, 52, 136
concordialis, 33
forsheyi, 33
oblonga, 9
putris, 8, 10, 52
unicolor, 33
wilsoni, 33
witteri, 33
sudanica, Biomphalaria, 15-24
tanganyikensis, Pseudospatha, 41
tannum, Campeloma, 42
Taxodonta, 49
tenagophila, Biomphalaria, 23
tentaculata, Bithynia, 13
texasiana, Polygyra, 34
thersites, Nassa, 133
tornescalis, Pallifera, 33
Trachydermon, 164
parvulus, 164
Trapezoideus, 41
Trichia, 8, 9, 11, 13
hispida, 8, 11, 13
sericea, 8, 9, 13
tridentatum, Carychium, 8, 9
Triodopsis, 50
multilineata, 50
Tritonia, 52
diomedia, 52
tropica, Lepidochitona, 164
tropicus, Bulinus, 45, 46, 56
tropicus, Isidora, 45, 46
Tropidiscus, 13
carinatus, 13
planorbis, 13
truncatula, Fossaria, 28, 31
truncatula, Lymnaea, 9
truncatus, Bulinus truncatus, 45, 46, 55, 56
truncatus, Isidora truncatus, 45, 46
truncatus sericinus, Bulinus, 45, 46
truncatus sericinus, Isidora, 45, 46
truncatus truncatus, Bulinus, 45, 46, 55, 56
truncatus truncatus, Isidora, 45, 46
tryoni, Aplexa hypnorum, 44
tunicata, Katherina, 37
ulvae, Hydrobia, 13
Uncancylus, 127, 130, 131
concentricus, 127, 130, 131
undatum, Buccinum, 13
unguis, Omalonyx, 48
unicolor, Succinea, 33
Unio, 41
Uniomerus, 42

Unionacea, 41
Unionidae, 41
Vallonia, 8, 9, 10, 11, 13
  costata, 9, 10, 11, 13
  pulchella, 8, 9, 13
Valvata, 13
  cristata, 13
  piscinalis, 13
velum, Hydatina, 133-135
ventricosa, Iphigena, 11
venustus, Philomycus, 33
vermeta, Catinella, 52
Vertiginidae, 1
Vertigo, 8, 10, 11, 33
  pusilla, 10
  pygmaea, 8, 10, 11
  rugosula, 33
  wheeleri, 33
verus, Mesodon, 34
virgata, Helicella, 13
virgata, Physa, 44
virginica, Crassostrea, 107
Vitrea, 8-11
  crystallina, 8-11
Vitrina, 9, 10, 13
  major, 9, 10, 13
Viviparus, 42
  georgianus, 42
  contectoides, 42
vortex, Spiralina, 13
vulgatus, Mesomphix, 34
wheatleyi, Glyphyalinia, 33
wheatleyi, Retinella, 33
wheeleri, Vertigo, 33
wilsoni, Succinea, 33
witteri, Succinea, 33
Zenobiella, 8, 10
  incarnata, 8, 10
Zonitoides, 13
  nitidus, 13

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